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Author:
Attwell, Joanna R

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The impacts of environmental visual noise on individual and collective behaviour

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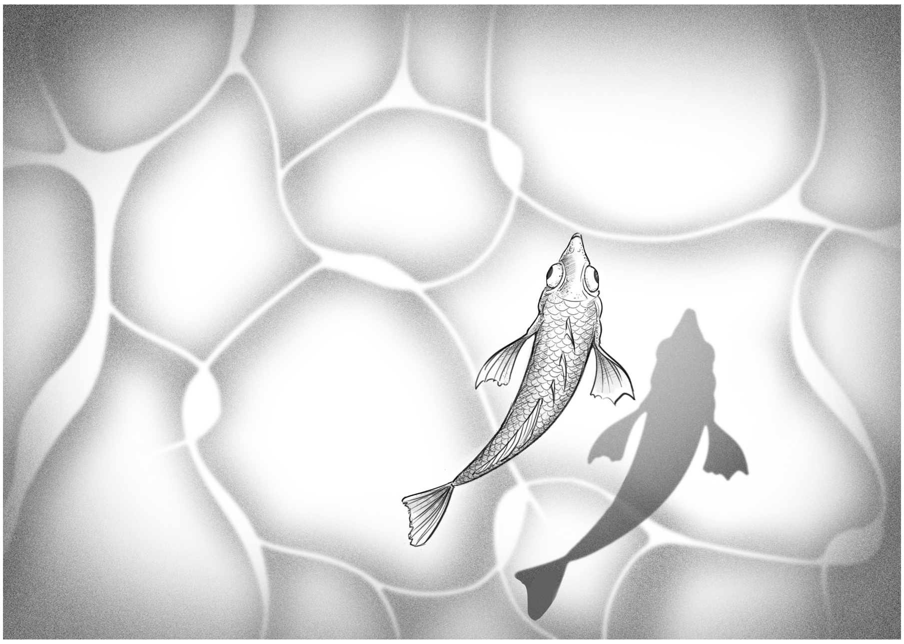
The Impacts of Environmental Visual Noise on Individual and Collective Behaviour

By

JOANNA ATTWELL

SUPERVISORS: Prof. Christos Ioannou, Dr. Chris Reid, Dr. Martin How,
Prof. Culum Brown, Dr. James Herbert-Read



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ABSTRACT

Ecological noise is an inherent part of all natural environments, with this noise often making it more difficult for animals to detect information. In this thesis I investigated the impact of two forms of dynamic visual noise on the behaviour of individuals and groups in two animal taxa. In Chapter 2 I found that a natural form of dynamic visual noise reduces the perception of three-spined sticklebacks (*Gasterosteus aculeatus*) and fish responded to this by selectively searching over more localised areas of their visual field. In Chapter 3 I found that fish had behavioural adaptations to mitigate the negative impacts of this noise by avoiding more visually noisy areas, and they achieved this by increasing their activity as a function of the locally perceived noise level. In Chapter 4 I asked whether pairs of fish compensated for some of the reduction in perception shown by individuals by adapting their social behaviour. I found no evidence to suggest that having access to social information improved the fish's collective ability to detect information in their environment and while there was some evidence that fish relied more strongly on social information in noisy conditions, my results suggested that the benefits of socially derived information in this system were limited. Finally in Chapter 5 I explored how a different form of dynamic visual noise affected pheromone laying behaviour, a source of social information, in weaver ants (*Oecophylla smaragdina*). I found that ants laid pheromone more consistently over time and showed greater preference for following a pheromone trail in higher levels of noise. Therefore ants could be increasing their reliance on social information in times of increased noise, allowing them to forage more effectively. My thesis demonstrates that animals have behavioural adaptations they can use to mitigate the impacts noise has on their perceptual abilities.

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I would firstly like to thank James Herbert-Read. Thank you for your guidance, enthusiasm and encouragements, without which I couldn't have completed this PhD. Thank you for all you have taught me, the time you have given me, and for your belief in my abilities from the beginning to end of my PhD. Secondly I would like to thank Christos Ioannou. Thank you for all the knowledge you have passed onto me and all you have taught me about being a good scientist, I feel I have learnt so much! Next I would like to thank Chris Reid, it was such a shame that I was never able to move over to Sydney for the PhD but I had such an amazing time visiting, thanks for being such a great host! Thank you for all you did for me at Macquarie and with working out a way for the experiments to still take place. I am so grateful to all three of my supervisors for all you have taught me and for the encouragements you have given me, I hope we will stay in contact!

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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: [redacted] DATE: 07/09/2022

This thesis is being submitted to Macquarie University and University of Bristol in accordance with the Cotutelle agreement dated 13/09/2018. To the best of my knowledge and belief, the thesis contains no material previously published or written by another person except where due reference is made in the thesis itself.

SIGNED: [redacted] DATE: 07/09/2022

PUBLISHED WORKS

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CHAPTER 1

INTRODUCTION

A version of this chapter is currently under review at the Journal of Experimental Biology.

1.1 Introduction

Gathering information is an essential task for organisms. Information reduces an organism's uncertainty about the state of the world, allowing them to make informed behavioural and physiological decisions to increase their survival and reproductive success (Dall and Johnstone, 2002). Indeed, the importance of information as a fitness-enhancing commodity is reflected in the myriad of biological sensors that have evolved including photo-, mechano-, olfactory-, auditory- and electro-receptors (Barth and Schmid, 2013). Incorporating these sensors with neural architecture has resulted in sensory modalities including vision (Goldsmith, 1990), olfaction (Hildebrand and Shepherd, 1997), audition (Naguib, 1996), and magnetic sensing (Wiltschko and Wiltschko, 2005). In addition to these passive forms of sensing, animals have evolved a suite of 'active sensing' mechanisms to sample information directly from the environment (Schroeder et al., 2010), including echolocation in bats (Griffin, 1958), mechano-reception in rodents (Bosman et al., 2011)) and electro-reception in fishes (Moller, 2002; Schumacher et al., 2016). These sensory modalities deliver a representation of the surrounding environment to an animal, allowing it to use this information to inform its behavioural decisions.

Signal detection theory suggests that sensory systems evolve to maximise detection of the signal of interest (e.g. olfactory cues from a target prey) against a background of noise (e.g. olfactory cues from other sources) (Wiley, 2013). While a greater number or sophistication of sensors allows animals to improve the signal-to-noise ratio, the sensory and neural machinery underlying these modalities are costly to both use and maintain. In humans, for example, the brain accounts for $\sim 20\%$ of resting metabolism (Attwell and Laughlin, 2001), largely due to the energetic costs associated with electrical transmissions (Niven, 2016). Vision is a particularly costly modality due to the information processing that is required to reconstruct visual scenes, accounting for 5 – 15% of a 1 - 8.5 g fish's resting metabolism (Moran et al., 2015). Active sensing demands further energetic investment, as signals or movements must be generated to sample information (Stamper et al., 2012). There is a trade-off, therefore, between having increased numbers of sensors to improve information detection and the metabolic costs of possessing them. Because of this trade-off, in addition to the physical constraints associated with bearing additional sensors and neural architecture (Chittka and Niven, 2009), animals are limited in the number and type of sensors they can invest in. All animals, therefore, can only gather finite amounts of information, giving them only a partial representation of the world around them. Environmental noise, therefore adds further uncertainty to both the transmission, reception and cognitive processing of information. In this review I discuss the impacts of environmental noise on the detection of information, and the mechanisms that animals have evolved to adapt to noisy conditions.

1.2 Information acquisition is confounded by environmental noise

An animal's ability to gather information about its environment is impeded by environmental noise. Environmental noise can be defined as any environmental stimulus that has the potential to interfere with the sensation of biologically meaningful cues or signals (Corcoran and Moss, 2017). Noise is typically associated with acoustic noise (Bateson, 2007; Kunc et al., 2016; Shannon et al., 2016; Slabbekoorn and Ripmeester, 2008), where weather, and human activities such as traffic noise, can generate varying intensities of background acoustic noise (Bee and Swanson, 2007; Halfwerk et al., 2011; Hatch et al., 2012; Hoskin and Goosem, 2010; Lampe et al., 2012; Moore et al., 2012; Morris-Drake et al., 2016; Nemeth and Brumm, 2010; Patricelli and Blickley, 2006; Picciulin et al., 2012; Slabbekoorn and Ripmeester, 2008; Tasker et al., 2010; Vasconcelos et al., 2007). But noise can occur in all sensory modalities (Figure 1). For example, the electric fields caused by lightning and the electro-pollution produced by power plants and power lines could disrupt communication and sensing in species that use electroreception (Benda et al., 2013). This noise could interfere with the detection of electrical signals by active sensors, as the frequencies of electrical noise can overlap with the electrical transmission frequencies of many species (Van der Sluijs et al., 2011). With chemoreception, the environment contains many chemicals that contribute to background noise, and these chemical cues can interfere with each other, for example artificially produced chemicals or scent marks made by another species. As well as background chemicals interfering with reception of odour cues, noise can be introduced during the transfer of chemical information. Odour molecules need to be transported through air or water, which is much slower and more stochastic than other forms of communication. Turbulence can break up this flow, disrupting the chemical signals being carried (Nehring et al., 2013). Turbulence as environmental noise could thus affect aquatic species such as sticklebacks, who use olfactory cues in long-distance mate attraction (Mclennan, 2003).

Noise can also occur in the visual domain. For example, visual information is degraded as light is scattered, filtered or absorbed through the viewing medium (Bradbury and Vehrencamp, 1989), particularly prevalent as turbidity in aquatic systems. Pike cichlid (*Crenicichla frenata*), for example, are less successful predators when hunting in more turbid environments (Ehlman et al., 2020). Spatially complex or moving backgrounds such as dappled light or water caustics (moving light bands that form on underwater substrates caused by the refraction of light through surface waves) (Matchette et al., 2018; Ord et al., 2007) add further noise to visual scenes. Human participants are significantly slower and make more errors when tasked with capturing moving prey items within simulated scenes containing dynamic illumination compared to static scenes (Matchette et al., 2018), and Picasso triggerfish (*Rhinecanthus aculeatus*) are slower to detect moving prey in the presence of dynamic water caustics relative to static water caustic controls (Matchette et al., 2020). The degree to which these types of noise can affect perception in an organism could depend on its visual acuity, temporal resolution and colour perception abilities (Bradbury and Vehrencamp, 1989).

More generally, environmental noise interferes with the detection of biologically relevant information through different pathways (Figure 1). When noise occurs in the same sensory channel as the information (uni-modal effects), noise can mask relevant information, making the information indistinguishable from the background noise. In particular, if the signal-to-noise ratio of an information source is below some critical threshold, then information will go undetected (Bateson, 2007; Wiley, 2013). Many species which use background-matching camouflage strategies make use of this pathway to reduce their chance of being detected by predators or prey (Cuthill et al., 2005; Pembury Smith and Ruxton, 2020). For other species, background noise can mask informative signals that are targeted towards receivers. For example, moving visual backgrounds impair the ability of Puerto Rican lizards (*Anolis cristatellus* and *A. gundlachi*) to detect territorial display signals (Ord et al., 2007), and anthropogenic acoustic sounds occurring in the same frequency domain as the calls of Lusitanian toadfish (*Halobatrachus didactylus*) reduce the ability of conspecifics to detect those calls (Vasconcelos et al., 2007). Hence, masking effects can impede the detection of both signals and cues, and in some cases these effects can be exploited by animals.

Noise can also interfere with the detection of biologically relevant stimuli by affecting the cognitive processes used in acquiring, processing or responding to information (Wiley, 2013). Unlike masking, 'cognitive interference' can occur when noise is generated in either the same or a different sensory channel to the information (cross-modal effects). Cross-modal noise can act as a distractor, focusing attention away from ecologically relevant information, and thereby reducing its detection. Caribbean Hermit crabs (*Coenobita clypeatus*), for example, are less responsive to potential threats when distracted by anthropogenic forms of acoustic and visual noise (Chan et al., 2010), and pallid bats (*Antrozous pallidus*) show similar reductions in successful foraging attempts when exposed to both overlapping and non-overlapping frequencies of prey sounds, suggesting distraction rather than masking effects are causing this decrease in foraging performance (Allen et al., 2021). When animals are tasked with processing information from multiple sensory modalities simultaneously, some sensory channels may be ignored altogether (Dukas, 2002), owing to the limited capacity of sensory systems to process all of the information they receive (Pashler and Sutherland, 1998; Skals et al., 2005). Noise can also induce stress responses (Sutherland et al., 2008), limiting an animal's ability to respond appropriately to information that may have been detected. Dwarf mongooses (*Helogale parvula*), for example, exposed to anthropogenic acoustic sounds have a reduced ability to respond to olfactory cues from predators (Morris-Drake et al., 2016), which is jointly attributed to both stress and distraction effects.

1.3 Cognitive and behavioural adaptations to noisy environments

Because noise impacts the ability of animals to detect or respond to information in their environment, animals have developed a suite of cognitive and behavioural mechanisms to either exploit or mitigate the impacts of noise on perception and decision-making (Figure 1). Indeed, the impacts of noise on information gathering can first be mitigated by investing in sensory machinery or cognitive processes to lessen the impacts of noise on perception. For example, investing in additional sensors increases the resolution of the signal compared to noise, which can lead to improved information detection (Figure 1). Such investments are likely to occur when the environmental source of noise is relatively stable in the environment, and natural selection can shape sensory and neural architecture over evolutionary time. Given the costs of investment in different sensory modalities, however, this may result in reduced investment in other sensory channels. For example, trade-offs in the investment of olfactory or visual information can result in different modalities being favoured depending on environmental conditions (Kiesecker et al., 1996; Mathis and Vincent, 2000; Montgomery and Merrill, 2017).

In addition to investing in additional sensors, animals may evolve cognitive mechanisms that filter out background noise during or after information has been gathered (Figure 1) (Kight and Swaddle, 2011; Pellegrino et al., 2017). Torrent frogs (*Odorrana tormot*), for example, can use ear tuning to specific frequencies of conspecific's calls thereby filtering out elements of background noise (Shen et al., 2010). Much like noise reduction algorithms in computer science that involve smoothing, or sampling information over extended periods of time, analogous cognitive mechanisms may change how information is sampled by sensors (Stöckl et al., 2016), or processed by the brain. Indeed, evidence for such cognitive processes comes from studies involving habituation, where animals that are initially exposed to sources of noise are unable to detect masked information, but, after prolonged exposure to noise, detection ability returns as cognitive noise reduction mechanisms are implemented. Such mechanisms are well known in the acoustic and chemical sensory channels, and appear to be an adaptive mechanism to filter out noise. Indeed, the rainforest cricket (*Paroecanthus podagrosus*), which experiences strong acoustic competition from background noise, exhibits more selective tuning that reduces background noise compared to their European counterparts where acoustic competition does not exist (Schmidt et al., 2011). The sensory filter of the rainforest species was also better able to increase the amplitude of the species specific frequencies against the background noise, making the relevant signals easier to detect (Schmidt et al., 2011).

Even without filtering out the background noise, animals may adapt the sensitivity threshold at which they initiate a behavioural response to information that is detected. Under conditions of increased noise, animals may increase this threshold (decreasing their sensitivity), reducing the likelihood of false positives (responses in the absence of a stimulus) (Chittka et al., 2009). Other cognitive strategies that can mitigate the effects of noise involve the use of search images, selectively searching for objects with known properties in noisy environments (Bond and Kamil, 2002; Dukas, 2004). Indeed, such pattern recognition algorithms (Sutherland, 1968) may improve the likelihood and speed at which objects are recognised amongst environmental noise.

However, many of the cognitive mechanisms used to mitigate the impacts of noise are costly in terms of the energetic investment needed to use or maintain the neural machinery behind such adaptations. Therefore, instead of using cognitive mechanisms to mitigate the impacts of noise, animals may instead adapt their behaviour to mitigate such impacts. Behaviourally, animals may select, or selectively avoid, areas of their environment with increased levels of noise. For example, prey species attempting to remain undetected from predators may preferentially select noisier environments, as those environments may offer increased camouflage opportunities. Indeed, least killifish (*Heterandria formosa*) select visually noisier backgrounds that mask their appearance under increased risk of predation (Kjernsmo and Merilaita, 2012). Environmental noise may also allow animals to explore more of their environment while remaining undetected. Larval pike (*Esox lucius*), three spined stickleback (*Gasterosteus aculeatus*), and fathead minnows (*Pimephales promelas*) show decreased anti-predator behaviour in more turbid water (Abrahams and Kattenfeld, 1997; Lehtiniemi et al., 2005), while Nile tilapia (*Oreochromis niloticus*) initiate foraging sooner as water turbidity increases (Wing et al., 2021), suggesting prey may exploit highly turbid environments to avoid being detected by visual predators (although see (Chamberlain and Ioannou, 2019)). On the other hand, predators may avoid areas of the environment where prey detection is more challenging (Attwell et al., 2021). Many species of bat, for example, avoid or spend less time foraging in acoustically noisier areas of their environment (Bennett and Zurcher, 2013; Gomes et al., 2021; Schaub et al., 2008) (but see (Bonsen et al., 2015)). Birds also avoid areas with higher acoustic noise and further to this are more likely to avoid areas where the acoustic frequencies of the noise overlap with that of local birdsong (Gomes et al., 2021). While controlling for abundance, bird foraging rates also decrease in higher noise areas (Gomes et al., 2021) suggesting that this avoidance of noise is because the search time for prey increases in noisy environments either due to masking or cognitive affects on attention, decreasing the profitability of prey in those areas (Erichsen et al., 1980). Ambient sounds also influence where acoustically active frog species choose to call. Anurans heavily rely on acoustics for reproduction, and the noise produced from fast flowing water can mask their vocalisations meaning that species may select which streams to call at (Goutte et al., 2013). Therefore, animals may avoid or exploit areas of the environment with increased noise, affecting foraging decisions or to reduce the likelihood of being predated.

Avoiding areas with increased noise, however, is not always possible. To mitigate the effects of noise on their perceptual abilities, animals often need to adapt how they gather information in noisy environments. To do this, individuals may search over smaller regions of their environment in noisy conditions, trading-off the likelihood of detecting information in the sampled area with their overall sensory range. Arctic grayling (*Thymallus arcticus*), for example, narrow their visual search angles when there is an increase in moving background debris in their visual fields (O'Brien and Showalter, 1993), as doing so increases perceptual ability in the restricted area of the visual field (Eriksen and Yeh, 1985). Further, because many animals do not continually sample information from their environment, instead sampling information in discrete bouts (either through saltatory eye- or whole-body movements), animals may adapt the timing of these searches to sample more or less frequently in noisy conditions. Adding increased pauses into search strategies, for example, reduces times of self-induced motion blur, increasing the capacity of sensory systems to detect information (Kramer and McLaughlin, 2001; O'Brien et al., 1990). For animals that use active sensing mechanisms, adapting how they gather information from their environment also affords another possibility to mitigate the impacts of noise. Bats, for example, increase the amplitude, duration, and number of echolocation calls produced in noisy conditions, resulting in an increase in detectability of their prey (Luo et al., 2015). Similarly *Eigenmannia virescens*, a species of weakly electric fish, increases the number of whole-body oscillations and tails bends when in the dark and when electrosensory cues become harder to detect (Stamper et al., 2012). These body movements can enhance the electrosensory perception in this species (Nelson and Maciver, 1999; Stamper et al., 2012). Adapting when, where or how information is sampled from their environment can therefore allow animals to compensate for an otherwise reduced information detection ability under conditions of increased noise. However, such changes to behaviour may also be costly in terms of energy expenditure or time allocated to detecting information in noisy environments. Could there be further ways, therefore, that animals could behaviourally mitigate the impacts that noise has on their ability to make adaptive decisions?

1.4 Social solutions to the impacts of environmental noise on perception

One way for individuals to further mitigate the impacts of environmental noise on perception and decision-making would be to share the burden of information processing with other individuals. This can be achieved for group-living animals, as group living offers individuals increased access to social information. By pooling imperfect estimates of the world around them, individuals in groups can make more accurate decisions than they could if alone (Garnier et al., 2007; Ioannou, 2017; Sumpter and Pratt, 2009). Pooling of information within groups may be particularly useful in noisy environments as a cheap means to mitigate the impacts of noise without requiring costly behavioural or cognitive adaptations. Grunbaum et al. (1998) used both agent-based and analytical models of collective decision-making to demonstrate that pooling of imperfect estimates by individuals in groups could allow groups to climb noisy environmental gradients that individuals on their own could not detect. Groups could collectively achieve this because individuals' imperfect directional estimates cancelled each other out, analogous to the many-wrongs principle of decision-making, leading to more targeted taxis of groups (Berdahl et al., 2018; Grünbaum, 1998; Simons, 2004). In an empirical extension of this work, Berdahl et al. (2013) demonstrated that larger groups of golden shiners (*Notemigonus crysoleucas*) were better able to track darker regions of their environment (which these fish prefer) even when this darker region was surrounded by noisy visual features (Berdahl et al., 2013). The fish achieved this by coupling social interactions with a decision rule that made them slow down when encountering darker, more favourable, locations. Using these rules, groups of fish could navigate an environmental gradient to reach a preferred local minimum, even though individuals on their own could not. Relying on this form of 'distributed sensing' allows groups of animals to outperform individuals in detecting information in noisy conditions.

An advantage of collecting information as a group is that animals might efficiently distribute information gathering between one another to improve their collective likelihood of capturing sparse information. For example, because individuals have limited and anisotropic sensory ranges, if they can distribute their search patterns to sample information from different regions of the environment, this could increase the likelihood that at least one individual detects information. Indeed, many ant species use chemical pheromone trails that indirectly coordinate each other's activity. This enables information about the environment to be built up over time, meaning that colonies can more efficiently allocate foragers to food sources (Hölldobler et al., 1990). MacGregor et al. (2020) found that sticklebacks (*Gasterosteus aculeatus*) in groups in swarm-like configurations (where individuals faced in different directions) were quicker at identifying the appearance of prey than groups that were more polarised (MacGregor et al., 2020). Given that such disorganised 'swarm-like' configurations can result from individuals decreasing their speed, or aligning with fewer group members, simple changes to individuals' movements or social interactions could shift groups into configurations that are more effective at gathering information in conditions of increased noise. Indeed, juvenile seabass (*Dicentrarchus labrax*) in acoustically noisy environments become less directionally ordered and less correlated in their movements (Herbert-Read et al., 2017). Although the authors of this study suggested that such noise could be impairing the ability of individuals to coordinate their movements, this could instead be an adaptive mechanism to distribute information gathering more effectively in times of increased perceptual constraints.

Individuals in groups could also adjust the timing of when each group member gathers information in noisy conditions to reduce the periods when information is not being gathered. As mentioned previously, individuals do not process information continually from their environment, instead gathering information in discrete sampling events that may relate to saltatory, self-induced, or saccadic eye movements (Gomez-Marin et al., 2011; O'Brien et al., 1990, 1989). An interesting possibility is that individuals in groups asynchronise the timing of their sampling events to be less overlapped in times of increased noise. Much like the alternation of vigilance bouts (Pays et al., 2012), such timing may reduce the periods of time when information gathering is compromised, leading to more efficient information gathering under noisy conditions.

Animals may also increase their reliance on sharing information in times when their perception becomes compromised. For example, *Lasius niger* ants in low light environments (where their visual perceptual abilities are reduced) increase pheromone deposition rates, and are more likely to follow pheromone trails than rely on their own navigation memory (Jones et al., 2019). Similarly, in well-lit conditions *Formica pratensis* ants use private information in the form of visual memories to navigate, but prefer social information in the form of pheromone trails at night (Beugnon and Fourcassie, 1988; Fourcassie and Beugnon, 1988). Changing the reliance on social information in times of compromised detection of private information suggests animals can use a flexible strategy to weigh other sources of information when their own perceptual abilities are compromised. Overall, therefore, animals may adapt their social behaviour to increase the likelihood of detecting and sharing information in times of increased environmental noise.

1.5 Thesis structure

In this thesis, I investigate the impact that a form of dynamic visual noise has on the behaviour of individuals and groups. I first test whether different levels of visual noise impact the visual perception of individual fish (sticklebacks, *Gasterosteus aculeatus*) (Chapter 2). I then explore whether fish adapt their behaviour to mitigate some of the impacts that noise has on individuals' perception, exploring whether fish avoid areas of increased noise in their environment (Chapter 3). Next, I look at whether fish adapt their social behaviour in times of increased visual noise, and ask whether this improves their collective ability to detect information in their environment (Chapter 4). Finally, in Chapter 5, I explore how another form of dynamic visual noise affects social information use in weaver ants (*Oecophylla smaragdina*). Overall, my thesis investigates the way dynamic visual noise impacts perception and assesses the behavioural strategies animals and groups use to mitigate such impacts.

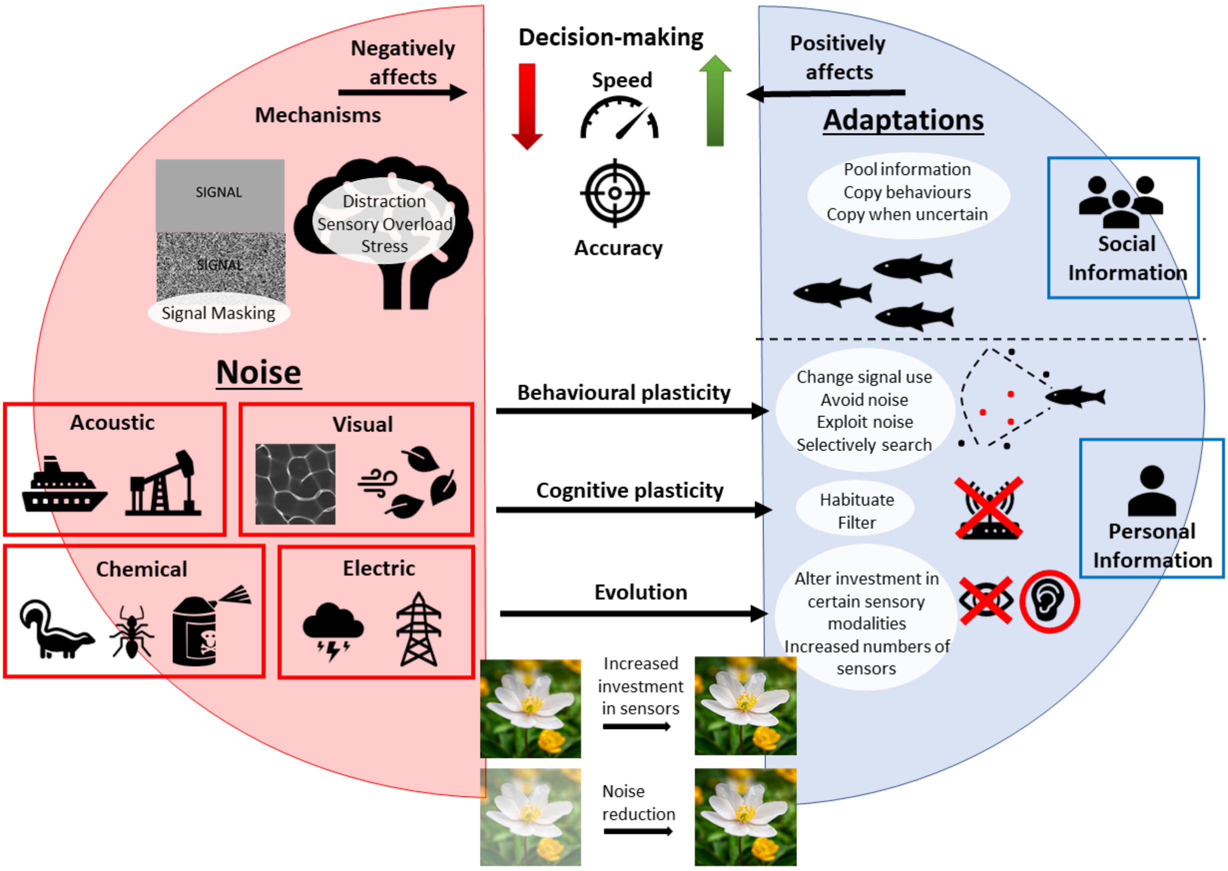


Figure 1.1: Schematic showing the impacts of different types of noise on information gathering and adaptations animals can use to mitigate this. Noise can negatively impact the detection of information in the environment through affecting the signal itself or through impacting cognitive processes. Animals can use different methods to mitigate the impacts of noise, either through their own personal information gathering or by using social information. These adaptations can help mitigate the negative impacts that noise has on the speed and accuracy of decision making, ultimately affecting individuals' survival and reproductive success.

CHAPTER 2

VISUAL NOISE REDUCES VISUAL PERCEPTION IN THREE-SPINED STICKLEBACK

Parts of this chapter are published in the following manuscript (along with the whole of Chapter 3): Attwell, Joanna R., Ioannou, Christos C., Reid, Chris R., and Herbert-Read, James E. (2021). Fish avoid visually noisy environments where prey targeting is reduced. *American Naturalist* 198(3), 421-432

The environment contains different forms of ecological noise that can reduce the ability of animals to detect information. Here I ask whether dynamic visual noise affects the visual perceptual abilities of individual fish by assessing their ability to detect virtual prey in environments with different levels of noise. To do this, I immersed three spined-sticklebacks (*Gasterosteus aculeatus*) into environments with a simulated form of naturally occurring visual noise termed *caustics* – moving light bands that form on underwater substrates caused by the refraction of light through surface waves. I first tested whether varying the flicker speed of this visual noise affected the likelihood that fish detected the prey, with higher flicker speeds equating to increased levels of visual noise. Following this, I asked whether the angle and range over which fish detected the prey was affected by different levels of visual noise. I finally investigated how different levels of visual noise affect the fish's movements when searching for prey. Fish were less likely to detect the virtual prey at higher levels of visual noise. Moreover, visual noise reduced both the range and angles of the visual field over which prey were detected. Noise did not affect the response latency of the fish to detect prey. If the fish are required to have consistently fast response times when searching for fast moving prey, this finding could suggest that fish are reducing the area over which they are searching until it is reduced to such a degree that their ability to respond to prey in their search area is not compromised. Therefore this reduction in the visual field of the fish could be an adaptive response to improve detection of prey in a smaller area without compromising on response latency. Fish had more movement bouts, accelerated more quickly and had a higher minimum speed when in higher levels of noise, but were also less likely to detect the prey when they were swimming more quickly. My results indicate that a natural form of dynamic visual noise reduces the perceptual ability of individual fish, but that fish could be altering how they search noisy environments to mitigate the impacts that visual noise has on their perceptual abilities.

2.1 Introduction

Natural habitats contain many forms of background noise, where noise can be defined as any environmental stimuli that have the potential to interfere with the sensation of biologically meaningful stimuli (Chapter 1) (Brumm, 2013; Corcoran and Moss, 2017; Cuthill et al., 2017). The most commonly documented forms of noise take visual or acoustic forms, for example, turbidity (Chamberlain and Ioannou, 2019), weather, and both marine and terrestrial traffic noise (Lampe et al., 2012; Tasker et al., 2010; Vasconcelos et al., 2007). These forms of environmental noise can interfere with the detection of ecologically meaningful stimuli primarily through two, non-mutually exclusive mechanisms. First, noise can mask the stimulus when the stimulus occurs in the same sensory channel as the noise (Bateson, 2007; Vasconcelos et al., 2007). Here, the detectability of a stimulus is determined by its signal-to-noise ratio; the strength of the informative signal with respect to unwanted background interference (Wiley, 2013). If noise in the environment increases, the signal-to-noise ratio of the stimulus is reduced, making the stimulus harder to detect (Wiley, 2013). Noise can also affect the cognitive processes used when processing information, distracting or confusing an animal (Wiley, 2013). Failing to detect biologically important information will have negative impacts on an animal's survival and fitness. For example, noise in the environment can reduce the ability of animals to communicate with conspecifics (Bee and Swanson, 2007; Fleishman, 1986; Lampe et al., 2012; Ord et al., 2007; Peters et al., 2007; Slabbekoorn and Ripmeester, 2008; Vasconcelos et al., 2007), to respond to predatory attacks (Morris-Drake et al., 2016; Wale et al., 2013), and to detect prey or forage efficiently (Azeem et al., 2015; Evans et al., 2018; Matchette et al., 2019; Party et al., 2013; Purser and Radford, 2011; Siemers et al., 2007; Wale et al., 2013).

Animals have evolved strategies to mitigate the impacts of noise on their perceptual abilities. One way predatory species do this in the visual domain is by using search images, whereby predators selectively search and focus their attention on common types of prey, increasing their probability of detecting those prey types in visually noisy scenes (Bond and Kamil, 2002; Dukas, 2004). Blue jays (*Cyanocitta cristata*) searching for digital moths, for example, are better at detecting common cryptic prey types, suggesting the use of a search image that can detect prey in noisy backgrounds (Bond and Kamil, 2002). Individuals can also choose to search areas more thoroughly but at the cost of reduced exploration. Arctic grayling (*Thymallus arcticus*) narrow their search angles when there is an increase in either current velocity or prey crypticity (O'Brien and Showalter, 1993). Focusing on a narrower visual angle when attention is limited improves information gathering in that area of the visual field (Eriksen and Yeh, 1985). Furthermore, some animals forage in a saltatory search pattern, interspersing their movements with short pauses (O'Brien et al., 1990, 1989). Adding increased pauses into search strategies reduces times of self-induced motion blur (Kramer and McLaughlin, 2001; O'Brien et al., 1990). This can increase the perceptual ability of animals by increasing the capacity of sensory systems to detect relevant stimuli which in turn increases the amount of information gained about prey, predators and obstacles in the environment (Kramer and McLaughlin, 2001).

While animals have behavioural adaptations to increase their likelihood of detecting information in noisy environments, most of this work has been done with static forms of visual noise. Visual noise, however, can also vary dynamically in the environment. Wind blown vegetation, dappled light (Matchette et al., 2019), and light scattered by water bodies can create backgrounds with dynamically changing illumination (Matchette et al., 2020, 2018; Ord et al., 2007). Little is known about how such dynamic visual noise affects perception and behaviour. Here I ask how visually dynamic backgrounds affect the ability of three-spined stickleback (*Gasterosteus aculeatus*) to detect virtual prey. Moreover, I ask whether these fish adapt their behaviour to potentially improve their ability to detect prey under more visually noisy conditions. Sticklebacks are a small (2 - 6 cm standard length) fish found in shallow marine and freshwater environments. They actively search for their prey of fish fry, small insects and crustaceans among the substrate and in the water column. They themselves are predominantly predated by birds and larger fishes, such as pike (*Esox lucius*) (Wootton, 1984). To investigate the impact of dynamic visual noise on sticklebacks' perception and behaviour, I used a simulated form of a naturally occurring source of dynamic visual noise called 'caustics'. Caustics occur in shallow aquatic environments and are formed from the diffraction and refraction of light through surface waves that is projected through the water column onto the substrate below (Lock and Andrews, 1992). Caustics are composed of 'a mosaic of polygonal patches that are irregularly enclosed by high-intensity light' (Matchette and Herbert-Read, 2021) and changes in water depth and properties of the surface waves can cause these caustic patterns to vary in their spatial distribution, intensity and flicker speed (Lock and Andrews, 1992). This form of dynamic illumination can reduce the likelihood of humans detecting a target on a computer animated display (Matchette et al., 2018), and can increase the latency of triggerfish (*Rhinecanthus aculeatus*) to attack a moving target (Matchette et al., 2020).

I first investigated whether visually noisy environments affected the ability of sticklebacks to detect prey by quantifying the likelihood that individual sticklebacks responded to virtual prey in environments with different levels of visual noise. A reduction in the number of responses by fish to the prey as a function of noise could either indicate that i) noise is acting as a perceptual constraint, or ii) that noise was acting as a motivational constraint. To separate these two hypotheses, I assessed how the angle and distance to the detected prey changed as a function of noise. I predicted that if noise was acting as perceptual constraint in higher noise levels the range over which prey could be detected (i.e. the angles and distance at which prey were detected in the visual field) would decrease. On the other hand, if noise was only acting as a motivational constraint, then only the likelihood, but not the range, of detection would decrease in higher levels of noise. I also measured the response latency of reactions to the prey, predicting that noise may impair the time taken to react to the prey. Furthermore, I predicted that fish would be less likely to detect prey when fish were moving at faster speeds, as motion blur is thought to reduce an animal's visual perceptual abilities (Land, 1999). Finally, I asked whether sticklebacks changed their search strategies in different levels of visual noise. I predicted that in higher levels of visual noise, the fish would have longer stationary search periods between movements. Moreover, I predicted that fish would have sharper accelerations and slower average swimming speeds in higher levels of visual noise to reduce the time periods when their perception was further compromised by self-induced motion.

2.2 Methods

2.2.1 Playbacks

Video playbacks of simulated caustics were projected on to the floor of an experimental arena (Figures 2.1 and 2.2) using a projector (see section 2.2.3). The playbacks were produced using Caustics generator Pro (DualHeights, 2018) by creating a series of 600 images of caustic patterns (3840 by 2159 pixels) (see software settings Table 2.1). These images were then stitched together in MATLAB 2018a to create smooth animations of moving caustics without the caustics appearing to spatially or temporally 'jump' when joined together. I created six animations that were made to vary in their amount of dynamic visual noise, or flicker speed. This was achieved by looping through the 600 images at different speeds, so that the slowest to fastest animations took 80, 40, 20, 10, 5 and 2.5 seconds, respectively, to complete a full loop. I classified the faster looping playbacks with higher flicker speeds as having higher levels of visual noise. I did not manipulate any other properties of the caustic patterns such as the spatial fractal nature of the caustics as this would have changed the total light intensity within the animations. Due to this, only the flicker speed of the caustics was manipulated.

Table 2.1: Parameter settings used in Caustics Generator pro to create the caustics

Parameter settings	**values**
Depth	5
Intensity	0.05
Amplitude filter	1.36
Frequency filter	1.5
Time filter	40.06

Virtual prey in the form of moving red dots (similar to Duffield and Ioannou (2017); Ioannou et al. (2019)) were then overlaid on the caustics. These prey were added in MATLAB after the caustic images had been looped together. Each prey appeared as a looming stimulus at a random location within the arena. Over a two second period, the prey increased in size from 0 to 12.5 mm diameter within $\frac{3}{4}$ of a second, maintained 12.5 mm diameter for ~ 1 second, and then shrank to ~ 6 mm before disappearing. The prey moved on a correlated random walk at 1.4 m s^{-1}. Often the prey would appear far from the fish's location, and pilot experiments confirmed that the prey were difficult for the fish to detect. To increase the number of prey detection events, therefore, each noise level contained 50 individual prey presentations (300 presentations within a single trial), with four seconds between the end of one prey presentation and the start of another. The limited presentation time of the prey was designed to allow the fish to detect and swim towards the prey, but reduce the likelihood of the fish sampling the prey and learning that they were not edible. The sticklebacks were fed red bloodworm in their housing tanks and were therefore highly responsive to these red dots. They would often peck at them if they got close, mimicking natural feeding behaviour and therefore did not need to be trained to attack the virtual prey.

Six playbacks (named a-f) were created where each playback contained each level of noise. Each noise level occurred at different times (order-within-trial) in the playbacks arranged in a latin square design (see Table 2.2). Transitions were added between each level of noise, so that there was a smooth transition between the different caustic speeds of each noise level. This involved creating animations that increased or decreased in speed from one noise level to another, which were subsequently placed between the respective animations of visual noise with the prey. Within these transition periods, no prey were projected. Each level of noise lasted for 320 seconds, with each transition period lasting between 70 and 90 seconds. This meant that in total, each playback lasted for ~ 50 minutes and 45 seconds. Each playback was presented once per day and at different times of the day (between 9am and 5pm) on different days.

Table 2.2: Order that the different levels of noise were presented within each playback for the virtual prey experiments. The letter above each of the columns is the name of the playback. One playback was given to each fish and each noise level occurred at all different times in the six playbacks in a latin square design.

Order within trial	**Playback**					
	a	**b**	**c**	**d**	**e**	**f**
1	2	3	1	6	4	5
2	4	1	5	2	6	3
3	1	5	4	3	2	6
4	6	4	3	1	5	2
5	3	6	2	5	1	4
6	5	2	6	4	3	1

2.2.2 Ensuring playbacks of caustics were consistent with natural conditions

I ensured that the speed of the moving light bands fell within the natural range of wave speeds that occur in nature. To measure this, I recorded the playbacks as they were projected into the arena using a camcorder (Panasonic HC-VX870) at 25 frames per second and 4K resolution located

2.15 m above the centre of the arena. I also recorded a video of a static frame of the playbacks. These seven videos (one for each playback and the static frame) were then imported into MATLAB (2018a), where I used an optical flow analysis to measure the spatial and temporal dynamics of the projected caustics using the function opticalFlowLK. This function detects the speed and direction of displaced pixels between frames in a video by giving displacement vectors of seemingly moving regions (Figure 2.1a). I then converted these displacement vectors into real world displacements, using the known pixel to mm conversion ratio, determined with a calibration board. I calculated the speed of displacement (in mm s^{-1}) across all regions within the arena in the six different playbacks separately.

Across all playbacks, the distribution of speed of the displaced pixels across the arena showed a strong peak close to 2 - 3 mm s^{-1} with a heavy right tail (Figure 2.1b). The median speed of the top ten percent of the displacement vectors increased as a function of the speed of the playbacks, with the median displacement of the slowest playback being 13.5 mm s^{-1} and the fastest playback being 109.9 mm s^{-1} (Figure 2.1c). Francis (1951) simulated natural wave speeds in a wind tunnel with a water depth of 15 cm (the same as in the experiments in my arena) and the range of wave speeds with varying wind conditions was found to go up to approximately 1 m s^{-1} (Francis, 1951). The movements of the caustics within the playback videos, therefore, were within this range, as the speeds of the caustics is proportional to the speed of these surface waves.

To ensure the light intensity was consistent across the different playbacks, I projected the same frames (n = 36 frames) from playbacks of the lowest noise level, an intermediate noise level, and highest noise level into the arena and measured the average lux readings at five different locations in the arena for 10 seconds. This gave a total of 180 lux readings for each of the noise levels. A HOBO MX2202 device was used to take the lux readings and was controlled from the HOBO mobile app. The device was configured to store a reading every second. I tested whether these lux readings differed between the noise levels using a generalised linear model fitted with a negative binomial error structure using the glm.nb function from the MASS package (Venables and Ripley, 2002) in R (R Core Team, Version 3.5.1). This was due to the strong positive skew and over dispersion in the data. Assumptions of the model were checked using the standard diagnostic plots in R by plotting the residuals vs fitted values and by checking the dispersion using the blmeco package in R (Korner-Nievergelt et al., 2015). There was no significant difference between the light intensities of the lowest (94.4 lux; IQR = 213.0), medium (95.3; IQR=192.3) or highest noise levels (95.3; IQR = 182.6) (Figure 2.1d; GLM; z = -0.17, p = 0.86), confirming that my playbacks had equivalent average light intensities across noise levels.

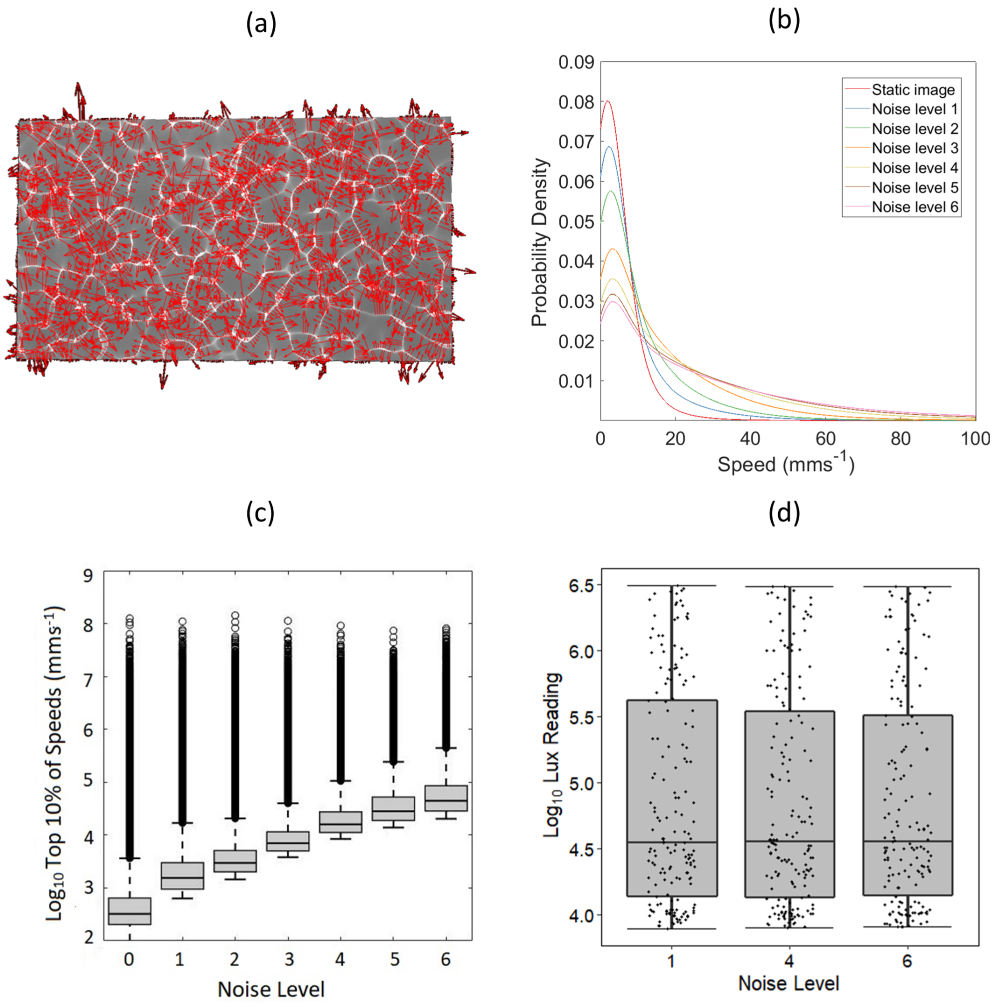


Figure 2.1: Quantifying the caustics properties and across the different playbacks. a) Displacement vectors of regions within an image that were determined to have moved between two subsequent frames. For plotting purposes, vectors were decimated by a factor of [10 10] and scaled by a factor of 10 b) Probability distribution of the speed of displacement vectors as a function of a static image and six different playbacks. c) Boxplot showing the distribution of the top 10% of the speeds of displacement vectors as a function of the static image and six different playbacks. d) Log lux readings taken across multiple frames in different locations for the lowest, medium and highest levels of noise. In c) and d) the central line of each box shows the median value while the upper and lower lines of the box show the upper and lower quartiles of the data, with whiskers extending to the upper and lower values not considered outliers (grey circles), points outside 1.5 × the interquartile range. Jittered points represent raw data points.

2.2.3 Study subjects and experimental arena

Three-spined sticklebacks (3.3 ± 0.4 cm; mean standard length ± SD) were caught from the river Cary in Somerton, Somerset, UK (51.069990 latitude,-2.758014 longitude) in March 2019. Caustics were observed in the same location as where the fish were caught. All fish were housed in glass housing tanks (40 x 70 x 35 cm, height x depth x width) for at least two months before experimentation. Approximately 40 individuals were kept in each tank on a flow-through re-circulating freshwater system with plastic plants and tubes for environmental enrichment. The fish were held at 14 ^{0} C under a 11:13 hour light:dark cycle and were fed bloodworms once per day, six days per week.

The tank used for experimentation consisted of a test arena (1.46 x 0.84 m, length x width) and a holding area (0.84 x 0.34 m, length x width). The holding area contained plastic plants and tubes for environmental enrichment. These two sections were separated by white opaque plastic (Figure 2.2) and both sections were filled to a depth of 15 cm. Water was filtered within the tank using a Eheim classic 600 External Filter on a flow-through re-circulating freshwater system and chilled to between 14.2 and 15.2^0 C using a D-D DC-300 chiller. Prior to each day of trials, fish that would be used in the subsequent day were placed in the holding area overnight, allowing them to acclimate to the conditions of the tank. Fish were not fed for 24 hours prior to experiments.

A BenQ W1700/HT2550 Digital Projector with 4K resolution operating at a 60 Hz vertical scan rate located 2.19 m above the arena (Figure 2.2)) projected the playbacks into the arena. The projections were played using a Dell Inspiron 15 notebook connected to the projector via a 4K HDMI cable located outside the experimental room. The experimenter was not present in the room while the trials were run. A camera (Panasonic HC-VX870) was placed 2.15 m above the centre of the test arena and filmed the trials at 4K resolution (3840 x 2160 pixels) at 25 frames per second. This camera was remotely controlled using the Panasonic Image App, operated by the experimenter outside the room. The arena was surrounded by black-out curtains to minimise the amount of external light entering the arena.

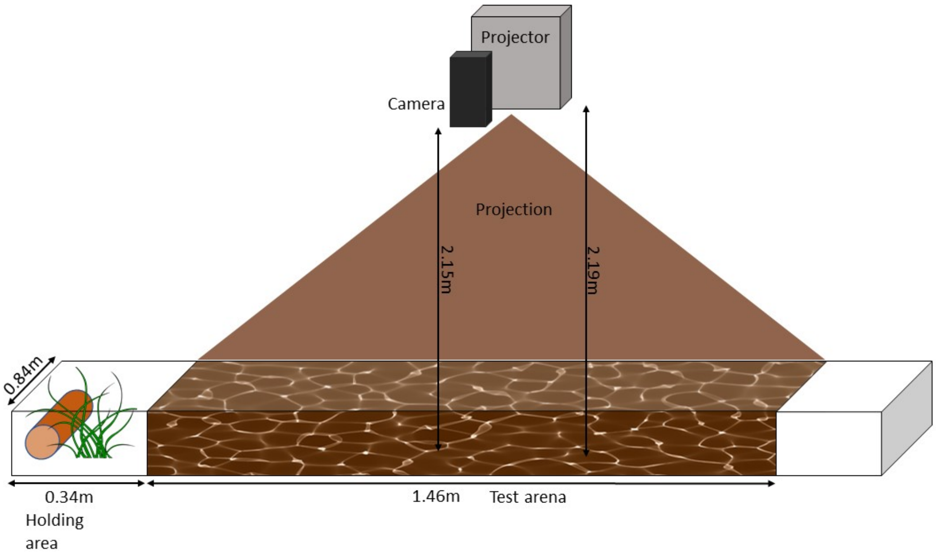


Figure 2.2: Schematic of the experimental set-up. The test arena made up the middle portion of the tank, with the caustics only projected into this section. To the left of the test arena was a smaller holding area separated by a perspex wall. Fish used in trials the following day were placed here the night before trials began. This area contained enrichment objects for the fish to help them acclimate to the conditions of the tank.

2.2.4 Experimental protocol

At the start of each trial, a single fish was moved from the holding arena into the test arena using a net and was allowed 10 minutes of acclimation time. During this time, the lowest level of noise was projected into the test arena before transitioning to the start of the playback. Individual fish then experienced six different levels of noise in combination with virtual prey that appeared and disappeared in random locations within the test arena for each trial (n = 108 fish in total). Experimented fish were then removed and placed in a separate housing tank to ensure that they were not reused between trials, and were then fed.

2.2.5 Behavioural scoring, tracking and analysis

Videos of the trials were firstly manually inspected to determine whether the fish detected each of the virtual prey. A detection was defined as when there was a noticeable change in the speed or direction of the fish towards the prey (similar to in Ioannou and Bartumeus et al. (2011)). Therefore, if the fish accelerated or decelerated while moving towards the prey, this counted as a detection. I quantified how many prey (out of a maximum of 50) the fish responded to in each level of noise within each trial. These changes in speed or direction could be misclassified as a detection if by chance the fish changed its speed or direction towards the prey without detecting it (i.e. false positives). To quantify the likelihood of false positives, for each experimental trial I simulated the appearance of a single virtual prey within a random location in the arena at a random time when there were no prey presented, within each level of noise in the trial (i.e. 648 simulated prey events, 108 events for each noise level). In these events, I asked whether my classification method would have scored the fish as detecting these prey (even though the prey were not there). This method allowed me to estimate the baseline level of false positives as a function of noise level. For the times when the fish did react to the prey, the response latency of the fish was measured. The time taken for the fish to respond to the prey was measured in seconds from the start of the prey presentation until the fish was classified as responding to the prey.

Fish in the videos were then tracked using Loopy (loopbio gmbh, 2015), a deep learning software which can be trained to detect specific points on an animal. In this case, I trained a model to detect the head and tail of the fish and tracked these points across each trial. The algorithm was trained on 65 frames for each of 7 videos to provide the software with reference images to learn from. The model was then applied to all videos, giving the x,y position of the head and the tail of each fish across all frames in all videos. These trajectories were used in the subsequent analyses.

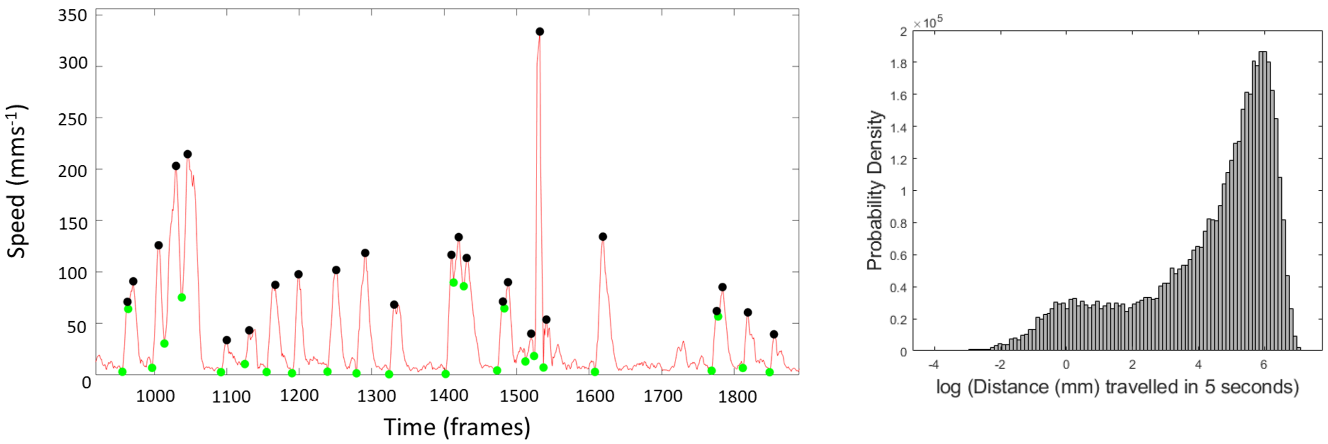
To explore how visual noise affects individual's perception of prey, I first needed to determine the locations of the prey relative to the fish in the recorded videos of the trials. To do this, before each trial, I projected a grid (51 x 29) of equally spaced white dots, with known coordinates created in MATLAB, into the test arena. A frame from this recording was then loaded into MATLAB for each trial. A script was then written to detect the white dots in the frame, providing the locations of the white points for each trial in the video. Next, the *estimateGeometricTransform* function in MATLAB was used to determine the projective transformation that would map the known coordinates of the white points defined in MATLAB to the points measured in the video frame. Using these transformation matrices, along with the known locations of the virtual prey as defined in MATLAB, I determined the prey locations as they would appear in the videos with the fish. Using this information, I then determined the angle and distance from the fish to the prey in 2D, based on a top-down view of the fish for each prey presentation event. The distance was calculated by taking the Euclidean distance from the fish's head to the prey location. The angle was calculated as the angle between the vector describing the heading of the fish, and the vector pointing from the fish's head to the prey's location. These angles ranged from 0 (prey directly ahead of fish) to a maximum of 180 degrees (prey directly behind the fish). The frame before the defined detection was used as the time-point to measure the angle, distance and swim speed for which the fish detected the prey. For instances when the fish did not detect the prey, the median response time (25 frames) when the fish did react to the prey was used as the time-point at which to measure these metrics.

The speed of the fish was calculated by taking the displacement in position of the fish between successive frames. Speeds were then smoothed using the *smooth* function in MATLAB with a moving average of 12 frames and using the Savitzky-Golay method with a 3rd degree polynomial. I interpolated over small gaps in the speed (12 frames or half a second) where tracking had failed using the function *interp1gap*. To explore whether the swim speed of the fish at the moment of prey presentation affected its likelihood of detecting the prey, the instantaneous speed that the fish was swimming at the time of detection, t, was calculated. This speed was taken as the distance the fish moved between frames *t-1* and *t*.

I also calculated the distance the fish was from the side of the arena when a prey presentation occurred so that this could be accounted for when exploring how noise influenced prey detection. If fish are closer to the side of the arena they may be less likely to detect prey. I calculated this distance by finding the nearest point between the fish and each four sides of the tank, calculating these distances and then saving the shortest distance.

I then calculated how the movements of the fish changed in different levels of noise. Sticklebacks swim with a saltatory motion, with intermittent bursts followed by stationary pauses (Figure 2.3a). Therefore, the speed profile of a fish is characterised by stationary periods followed by bursts of speed. These bursts can come in quick succession and are therefore associated with a minimum and maximum speed, along with acceleration and deceleration periods in between these troughs and peaks. These saltatory movements were analysed to explore whether the fish adapt their movement strategies in different levels of noise. To do this, I first calculated the proportion of time the fish spent stationary. Stationary periods were defined when the fish moved < 10 mm in five seconds which was $\sim 19\%$ of the data (see Figure 2.3b).

I then calculated the local maxima and minima in the speed of the fish during times they were moving. The *findpeaks* function in MATLAB was used to locate these peaks and troughs corresponding to the beginning and end of a movement bout or ‘decision’ by the fish (Figure 2.3a). Peaks had to be separated by more than six frames (a quarter of a second) and changes in speed from trough to peak that were less than 25 mm s^{-1} were not defined as a movement decision. Each trough and peak for each movement were paired together. I also calculated the acceleration associated with for each movement, and the number of movement decisions made per second. Median values for each of these four metrics were taken for each noise level for each individual in a trial.


(a)

(b)

Figure 2.3: a) Speed profile of the fish showing the saltatory motion. The red line shows the smoothed speeds of the fish. Black circles show the peaks and green circles show the troughs. b) Log of the distance travelled by the fish in five seconds. The cutoff for defining when the fish was stationary was taken from between the two peaks which was equivalent to 10 mm moved in five seconds.

2.2.6 Statistics

To test how the likelihood of detecting the prey was affected by the level of visual noise and the angle and distance to the prey, I used a generalised linear mixed model (GLMM) with a binomial error structure. The package glmmTMB (Brooks et al., 2017) was used for all GLMMs. The response variable was a binary variable of whether the fish detected the prey or not. Fixed effects included the interaction between noise and distance to the prey, the interaction between noise and the angle to the prey, the interaction between noise and the instantaneous swim speed of the fish, the prey number in the trial, the distance the fish was from the nearest side of the arena and the temperature of the water. Noise was added as a random slope, and trial (i.e. individual fish identity) was added as a random intercept. This random slope allows individuals to vary in how strongly noise impacts their detection, and the random intercept allows individuals to differ on average in how likely they are to respond to the prey.

For the response latency, I used a linear mixed model (LMM) to test if the response time of the fish was affected by noise. Response latency was square root transformed due to a positive skew in the data. The noise, distance to prey, angle to the prey, prey number and speed of the fish were all added as fixed effects along with the interaction between noise and distance to prey. Trial was added as a random intercept to allow individuals to differ on average in their response latencies, and noise was added as a random slope to allow individuals to vary in how strongly noise impacts their response latency. The model failed to converge with noise as a random slope, so I used the getME function in the package lme4 (Bates et al., 2015) to extract the parameter estimates for the fixed and random effects and then used the update function from the base stats package in R (R Core Team, Version 3.5.1) to run the model again starting from the parameter values extracted in the previous step. This then allowed the model to converge.

Linear mixed models were used to test whether noise level was a significant predictor of the proportion of time the fish spent stationary, the fish's median minimum speed (at the trough), median maximum speed (at the peak), median acceleration and the fish's median decision rate. The distribution of accelerations and minimum speeds of the fish were positively skewed so these variables were log transformed. Order within trial was added as a fixed effect and trial was included as a random effect for all models. Noise was not included as a random slope as the model would not converge, even after using the method described above.

All statistics were performed in R 3.5.1 (R Core Team, Version 3.5.1). The package lme4 (Bates et al., 2015) was used for all linear mixed models. Model comparison was performed using the *Anova* function in the car package in r (Fox and Weisberg, 2019). A Type II Anova was run with the Chi squared test statistic to test for an effect of all fixed effects. The full models were simplified by removal of non-significant terms before final analysis. The estimates and effect sizes (cohen's D) are presented in Table 2.3.

2.3 Results

Fish were less likely to detect prey in higher levels of visual noise (Figure 2.4; GLMM; $\chi^2 = 44.3, df = 1, p < 0.001$). Fish were less likely to detect prey at greater distances from them (Figure 2.5 a-d; GLMM; $\chi^2 = 1143.4, df = 1, p < 0.001$), and less likely to detect prey further behind them (Figure 2.5 e-h; GLMM; $\chi^2 = 255.5, df = 1, p < 0.001$). There was also evidence that increased noise acted as a perceptual constraint on the ability of fish to detect the prey, rather than just a motivational constraint. In higher levels of noise, the fish became even less likely to detect prey that appeared at further distances from them (interaction between noise and distance to prey: Figure 2.5d; GLMM; $\chi^2 = 37.3, df = 1, p < 0.001$). There was a non-significant trend that prey were less likely to be detected in more peripheral regions of the fish's visual field as noise levels increased (interaction between noise and angle to prey: Figure 2.5h; GLMM; $\chi^2 = 5.8, df = 1, p = 0.055$). Fish also became less likely to detect prey later on in the trial (GLMM; $\chi^2 = 279.2, df = 1, p < 0.001$), when they were swimming more quickly (Figure 2.6; GLMM; $\chi^2 = 48.0, df = 1, p < 0.001$), when they were closer to the side of the arena (GLMM; $\chi^2 = 25.8, df = 1, p < 0.001$) and when the temperature of the water was cooler (LMM; $\chi^2 = 11.7, df = 1, p < 0.001$). The effect of swim speed on prey detection became even greater in higher levels of noise, indicating that as speed and noise increased, it became even more difficult for the fish to detect the prey (interaction between speed and noise: Figure 2.6, GLMM; $\chi^2 = 22.5, df = 1, p < 0.001$). Our estimations of the number of false positives (classification that the fish detected the prey even if the prey had not been detected) were well below that observed in the detections of real virtual prey (Figure 2.4).

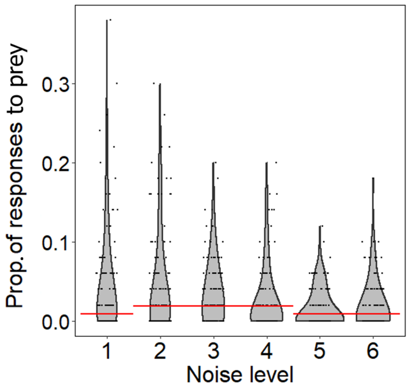


Figure 2.4: Responses to the virtual prey. Proportion of responses to the virtual prey out of the possible 50 prey presentations in each level of visual noise per fish (n = 108 fish in total). As the noise level increases the proportion of responses to the virtual prey decreases. The violin plot represents a mirrored probability density function, and each black marker represents an individual data point (responses for each fish within a noise level) jittered for clarity. The red lines show the proportion of false positives (false classifications) that were checked using the ‘simulated’ prey presentations.

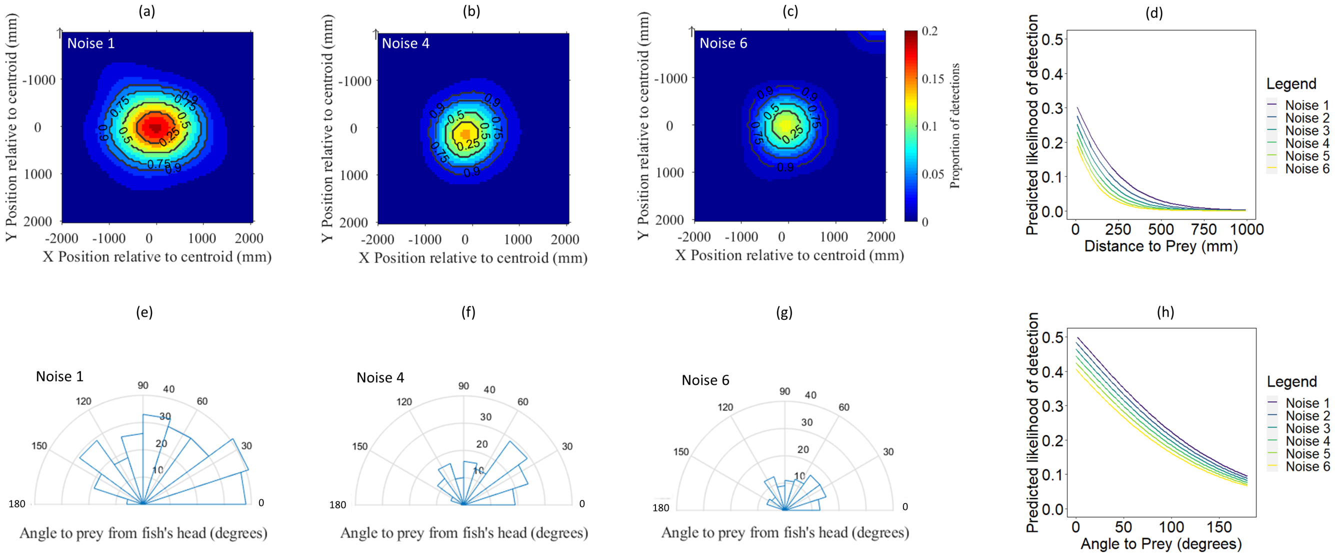


Figure 2.5: Changes in noise affect the likelihood sticklebacks detect virtual prey. a - c) Contour heat plots (average across all trials) showing the likelihood and range over which prey were detected in different regions of the fish's visual fields and in different levels of noise. The heat in each plots shows the proportion of responses to the prey divided by the total number of prey presentations in that region (~ 2 x 3cm) with the fish facing along the positive x axis. Hotter colours indicate areas where the fish is more likely to detect the prey. Contour lines mark the cumulative proportions of prey that were detected within that region. For example, 25% of the prey that were detected occurred within the inner contour marked 0.25. d) Plot showing how the predicted likelihood of a detection changes with the distance to the prey for each level of noise. The angle at which the prey appeared is fixed at 45 degrees within this plot. e - g) Rose plots across all trials showing the angles to the prey when the fish detected the prey. These angles ranged from 0 (prey directly ahead of fish) to a maximum of 180 degrees (prey directly behind the fish). The side of the fish that the prey was detected was not recorded. h) Plot showing how the predicted likelihood of a detection changes with the angle to the prey for each level of noise. The distance at which the prey appeared is fixed at 750 mm. Plots a) and e) are for noise level one, b) and f) are noise level four and c) and g) are noise level six. d) and h) are based on the statistical model predictions. The darkest line on each plot shows noise level one and the lightest colour shows noise level six.

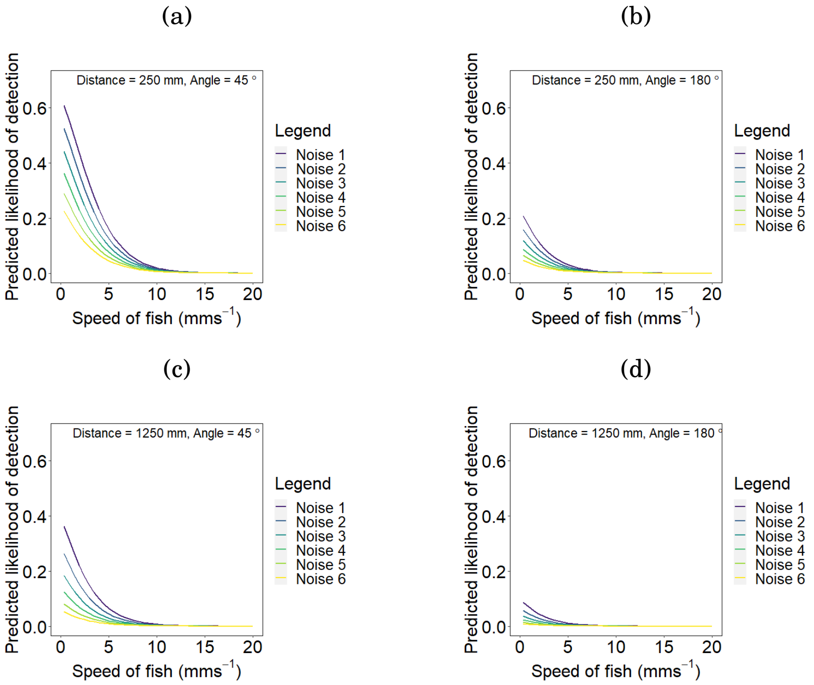

(a) (b) (c) (d)

Figure 2.6: Noise and self-induced motion affected the likelihood that fish detected virtual prey. Statistical model predictions showing how the likelihood of a detection decreased as fish swim speed increased and as noise level increased. The darkest line on each plot shows noise level one and the lightest colour shows noise level six. Each figure shows this relationship between speed and likelihood of detection, with the angle and distance to the prey fixed at different quantities a) Distance to prey fixed at 250mm and angle to prey fixed 45 degrees. b) Distance to prey fixed at 250mm and angle to prey fixed at 180 degrees. c) Distance to prey fixed at 1250mm and angle to prey fixed at 45 degrees. d) Distance to prey fixed at 1250mm and angle to prey fixed at 180 degrees.

While the likelihood of prey detection reduced in higher levels of noise, the noise level did not affect the time taken for the fish to detect the prey (LMM; $\chi^2 = 0.15, df = 1, p = 0.70$), and the angle at which the prey was detected was also not affected by this response latency (LMM; $\chi^2 = 1.23, df = 1, p = 0.27$). However the response latency was larger when prey were detected at greater distances (LMM; $\chi^2 = 104.0, df = 1, p < 0.001$) and when the fish were swimming at slower speeds (LMM; $\chi^2 = 4.0, df = 1, p = 0.045$). There was a negative interaction between noise and distance to the prey (LMM; $\chi^2 = 5.8, df = 1, p = 0.016$), meaning that in higher levels of noise the effect of distance on response latency is lessened.

Fish spent less time stationary in higher levels of noise (Figure 2.7; LMM; $\chi^2 = 11.5, df = 1, p < 0.001$). Fish increased the minimum speed of their movement bouts or 'decisions' in higher levels of noise (Figure 2.8a; LMM; $\chi^2 = 73.1, df = 1, p < 0.001$), however the level of noise did not affect the median maximum speed of the fish's movement bouts (Figure 2.8b; LMM; $\chi^2 = 0.3, df = 1, p = 0.59$).

The fish accelerated more quickly (Figure 2.8c; LMM; $\chi^2 = 9.4, df = 1, p = 0.002$) and had a higher decision rate (Figure 2.8d; LMM; $\chi^2 = 83.9, df = 1, p < 0.001$) in higher levels of noise. The minimum speed (LMM; $\chi^2 = 59.9, df = 1, p < 0.001$) and the decision rate of the fish (LMM; $\chi^2 = 94.8, df = 1, p < 0.001$) increased later on in the trial, and the acceleration (LMM; $\chi^2 = 27.2, df = 1, p < 0.001$) and proportion of time spent stationary (LMM; $\chi^2 = 37.2, df = 1, p < 0.001$) decreased later in the trial. There was no evidence that the order in the trial had an effect on the maximum speed swum by the fish (LMM; $\chi^2 = 2.8, df = 1, p = 0.1$).

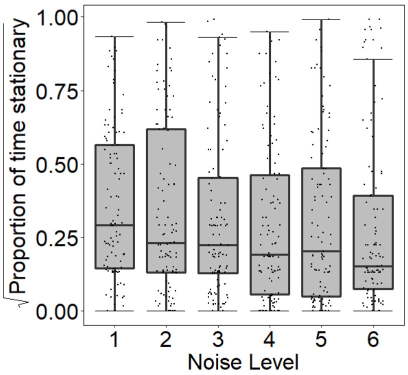


Figure 2.7: Fish spent less time stationary with increasing levels of visual noise. Square root of the proportion of time the fish spent stationary as a function of the noise level. The central line of each box shows the median value while the upper and lower lines of the box show the upper and lower quartiles of the data. The whiskers extend to the data points within 1.5 × the interquartile range. Jittered points represent raw data points.

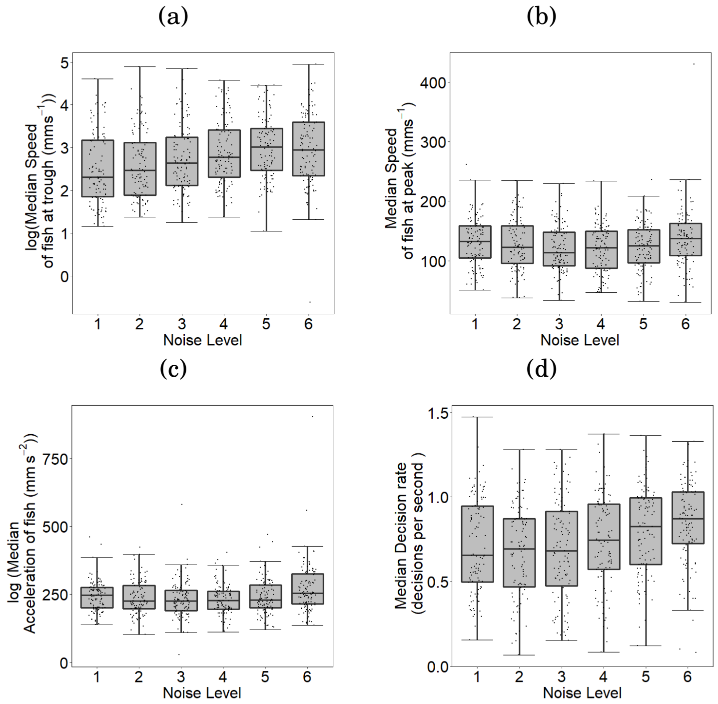


Figure 2.8: How fish changed their movement bouts or ‘decisions’ as a function of noise. a) Log of the median minimum speed of the fish (at the trough) for each decision. b) Median maximum speed of the fish (at the peak) of each decision. c) Median acceleration of the fish for each decision. d) Median decision rate (decisions per second). All medians were taken across all the decisions of one fish within one noise level for each trial. The central line of each box shows the median value while the upper and lower lines of the box show the upper and lower quartiles of the data. The whiskers extend to the data points within 1.5 × the interquartile range. Jittered points represent raw data points, each fish has one data point in each noise level.

Table 2.3: Estimates and Cohen's D for each of the statistical tests

Explanatory Variable	**Main Response variable**	**Estimate**	**Cohen D**
Detection (binary)	Noise	-1.4	-2.9
Detection (binary)	Distance to prey	1143.4	-3.0
Detection (binary)	Angle to prey	255.5	-2.6
Detection (binary)	Noise x Distance to prey (interaction)	37.3	-1.9
Detection (binary)	Noise x Angle to prey (interaction)	5.8	-1.8
Detection (binary)	Prey number within trial	279.2	-2.5
Detection (binary)	Swim speed	48.0	-0.9
Detection (binary)	Distance to tank	25.8	-0.8
Detection (binary)	Water temperature	11.7	-87.8
Response Latency	Noise	1.0	-1.6
Response Latency	Distance to prey	0.07	-2.2
Response Latency	Angle to prey	-0.008	-2.1
Response Latency	Swim speed	-0.02	-0.86
Minimum decision speed of fish	Noise	0.1	1.3
Minimum decision speed of fish	Order in trial	0.09	1.3
Maximum decision speed of fish	Noise	0.38	4.1
Maximum decision speed of fish	Order in trial	-1.16	4.1
Acceleration of decisions	Noise	0.20	4.9
Acceleration of decisions	Order in trial	-0.34	4.9
Decision rate	Noise	0.032	-2.3
Decision rate	Order in trial	0.034	-2.3
Proportion of time stationary	Noise	-0.015	- 2.7
Proportion of time stationary	Order in trial	-0.026	-2.7

2.4 Discussion

Fish were less likely to detect prey in more visually noisy environments. Moreover, fish were less likely to detect prey further behind them and at greater distances from them, with this effect becoming stronger in higher levels of noise, particularly for distance. Fish were also less likely to detect prey when they were travelling at faster speeds. Noise, however, did not affect the response latency of the fish to detect the prey. There was also evidence that fish changed their movement strategies in higher levels of noise, with individuals spending less time stationary, increasing their number of movement bouts, accelerating more quickly, and increasing their minimum swim speed in higher levels of noise.

As noise increased, the fish were less likely to detect the prey. This is consistent with other systems where humans, chicks and triggerfish took longer to detect prey on backgrounds with dynamic visual noise as opposed to static controls (Matchette et al., 2020, 2018, 2019). However, the likelihood of detecting the prey did not decrease evenly across all regions of individuals' visual fields. Instead, fish were less likely to detect prey further away and further behind them, with this effect increasing in greater levels of noise. This suggests that the noise is placing a perceptual constraint on individuals rather than being due to a reduction in motivation. Attention is a limited resource and individuals can choose how to allocate this limited attention to different tasks. It is attention that allows a predator to detect a prey item that otherwise might go undetected if attention is focused elsewhere. If it is indeed the case that noise is placing a perceptual constraint on these fish, individuals could be responding by focusing their attention on a smaller area of their visual field in higher levels of noise, i.e. at closer distances and narrower angles, thus being selective in their searching and improving their detection ability for this restricted area of their visual field (Eriksen and Yeh, 1985). Arctic grayling (*Thymallus arcticus*), for example, narrow their visual search angles when there is an increase in moving background debris in their visual fields (O'Brien and Showalter, 1993).

I found no evidence that the response latency for fish to detect prey was affected by noise. This is in contrast to other systems where underwater caustics cause triggerfish (*Rhinecanthus aculeatus*) to take longer to respond to prey when compared to static caustic controls (Matchette et al., 2020). The difference in my findings could be because of how the prey were presented. In

Matchette (2020) the triggerfish were required to search for a single moving prey item that was always present whereas in my experiment the sticklebacks were searching for moving prey which constantly appeared and disappeared. Across the literature the effect of noise on response latency appears to vary greatly depending on the system and species. Juvenile Damselfish (*Pomacentrus wardi*) take longer to respond to a looming predator stimulus when exposed to the noise of a 2-stroke engine compared to ambient noise, suggesting that anthropogenic acoustic noise is impacting the way that juvenile fish assess risk. However, there is no difference compared to ambient noise when exposed to a quieter 4-stroke engine (McCormick et al., 2018). Furthermore, sticklebacks respond more quickly to a visual predatory stimulus when acoustic ship noise is present compared to an acoustic control of an empty harbour without ship noise, while minnows show no change in their response latency (Voellmy et al., 2014). This variation in responses with noise could be due to how individuals accumulate information to make a decision. When making a decision, there is often a speed-accuracy trade-off that individuals can try to optimise according to the drift-diffusion model (Ratcliff, 1978). This model aims to achieve the quickest expected decision time with a desired expected error rate which can be achieved by varying decision thresholds. The threshold level most beneficial to an individual will depend on the relative costs and benefits for their particular context (reviewed in Marshall et al. (2017)). Here, it may be important for the sticklebacks to have consistently fast response times when searching for fast manoeuvrable prey. To achieve this in higher levels of noise the fish could reduce the area over which they are selectively searching until it is reduced to such a degree that their ability to detect prey in this restricted search area is not compromised. In this way, the range over which prey are detected may decrease in noise, while response latencies remain consistent with noise level.

The response latencies of the fish to detect the prey were affected by the distance to the prey and the swim speed of the fish. This could be due to the increased motion blur on the sticklebacks' retina when moving more quickly (Land, 1999) and objects at greater distances becoming harder to detect (Bradbury and Vehrencamp, 1989). Therefore if the stimulus intensity is reduced, the fish could be accumulating evidence more slowly making the decision time longer. The angle to the prey, however, had no effect on response latency which could be because of the wide visual range of these fish, meaning they can detect movement in a wide visual angle. Alternatively the lack of effect on response latency could be due to the way I measured a detection in the fish. I was only able to observe their physical behavioural response, where they show a change in direction or acceleration towards the prey. This therefore did not take into account the internal processing time between when the fish first cognitively became aware of the prey, and then decided to make a behavioural response towards the prey. To get a more accurate measure of how detection times are affected by noise, neurological recordings (e.g. Nicolelis et al. (2003)) or eye movements could be measured (Billington et al., 2020). This would however be very challenging in freely moving animals, and therefore my approach represents a good proxy for assessing detection times.

Fish were less likely to detect prey when they were swimming more quickly. This is likely due to the increased motion blur on their retina when travelling at faster speeds (Land, 1999), which makes it more difficult to detect moving objects. This effect was more pronounced in higher levels of noise adding further support to the idea that noise is affecting visual perception in these fish. It is surprising, therefore, that the fish increased several aspects of their activity in higher noise levels, namely their minimum swim speed, decision rate, and also decreased the time they spent stationary, while they did not reduce their maximum speed in higher levels of noise. It is perhaps unlikely, therefore, that fish were changing their saltatory search pattern to aid their perception, as most of these changes to movement would impede rather than aid visual search in noisy environments. Indeed, the only change in motion expected to improve visual perception was the increase in acceleration in the fish's saltatory search pattern, as this would decrease the time when the fish was actively changing speed, and therefore may reduce the time when there is excessive motion blur (Kramer and McLaughlin, 2001; O'Brien et al., 1989). Why, therefore, did fish increase their activity in higher levels of noise? Perhaps the increase in activity is a result of the fish increasing their exploration to increase their encounter rates with prey (see Chapter 3). This would be expected if the sticklebacks' explored their environment faster than the exploration rates of their prey. In the wild, sticklebacks feed on small insects and larvae, such as Chironomid larvae (Wootton, 1984), which the virtual prey in my experiment emulate. These prey are typically found amongst the substrate (Pinder, 1995), meaning that sticklebacks need to explore their environment in order to come into contact with this prey. Noise, therefore may affect the trade-off between exploration, energy expenditure of the search, and prey detection. For example, because noise makes prey less likely to be detected, sticklebacks may adapt their exploration strategies to mitigate the impacts of reduced detection by sampling more of their environment but at a lower likelihood of prey detection in those areas. Indeed, similar changes to search strategies are observed when predators are less likely to encounter or detect prey. Chinese salamanders

(*Cynops orientalis* and *Cynops cyanurus*), for example, change their search strategy depending on the availability of their prey. When prey availability is low, salamanders search more actively (more moves per time segment) and when prey availability is high, the salamanders switch to searching less actively with a more ambush style of hunting (Anthony et al., 1992). Similarly Black-legged Kittiwakes (*Rissa tridactyla*) increase the length of their foraging trips, and forage over a greater distance, when prey abundance is lower compared to years of high abundance (Suryan et al., 2000). Therefore the sticklebacks in my experiment could also be increasing their activity while foraging when prey are harder to detect. However increased activity is likely to incur energetic costs, but individuals may be willing to pay these costs if this increases encounter rates with prey. American Kestrels (*Falco sparverius*) switch to preferring hovering as a search strategy compared to other methods, as the energetic costs of hovering are reduced in high winds. Although this method still requires more energy than other search tactics, it leads to a greater prey capture per unit time (Rudolph, 1982). Therefore it is possible that the sticklebacks here could be choosing a more energetically costly method of searching to increase their encounter rate with prey.

It is also possible that fish use other strategies not measured here to mitigate the effects of reduced perception. Animals can switch to relying on other sensory modalities in visually noisy environments when their vision is compromised (Partan, 2017; Suriyampola et al., 2018). Female three-spined sticklebacks rely more on visual cues when choosing a mate in clear water, but in turbid water, where vision is compromised, they rely more on olfactory cues (Heuschele et al., 2009). Similarly, squirrels (*Sciurus carolinensis*) in acoustically noisy urban environments respond more to tail flagging than those in rural environments which suggests a multimodal shift from reliance on audio cues to visual signals in acoustically noisier environments (Partan et al., 2010). It is therefore possible here that the sticklebacks are using other adaptations to mitigate the effects environmental noise has on their perception. It would be valuable to test, for example, if the fish increase their reliance on olfactory cues in increased noise. This could perhaps be achieved by giving them a choice between a conflicting olfactory and visual cue in different levels of noise and seeing whether they switch which cue they choose when in different conditions.

In summary, my results demonstrate that a natural form of visual noise can place perceptual constraints on sticklebacks and reduce their likelihood of detecting prey. My results suggest that the fish reduce the areas they visually search in their environment in times of increased noise, although they do not appear to adapt their saltatory search patterns in a way that would lead to an improvement in perceptual ability. Instead, fish appear to be increasing their exploration to potentially encounter more items of prey, albeit with those prey being less likely to be detected.

2.5 Appendix

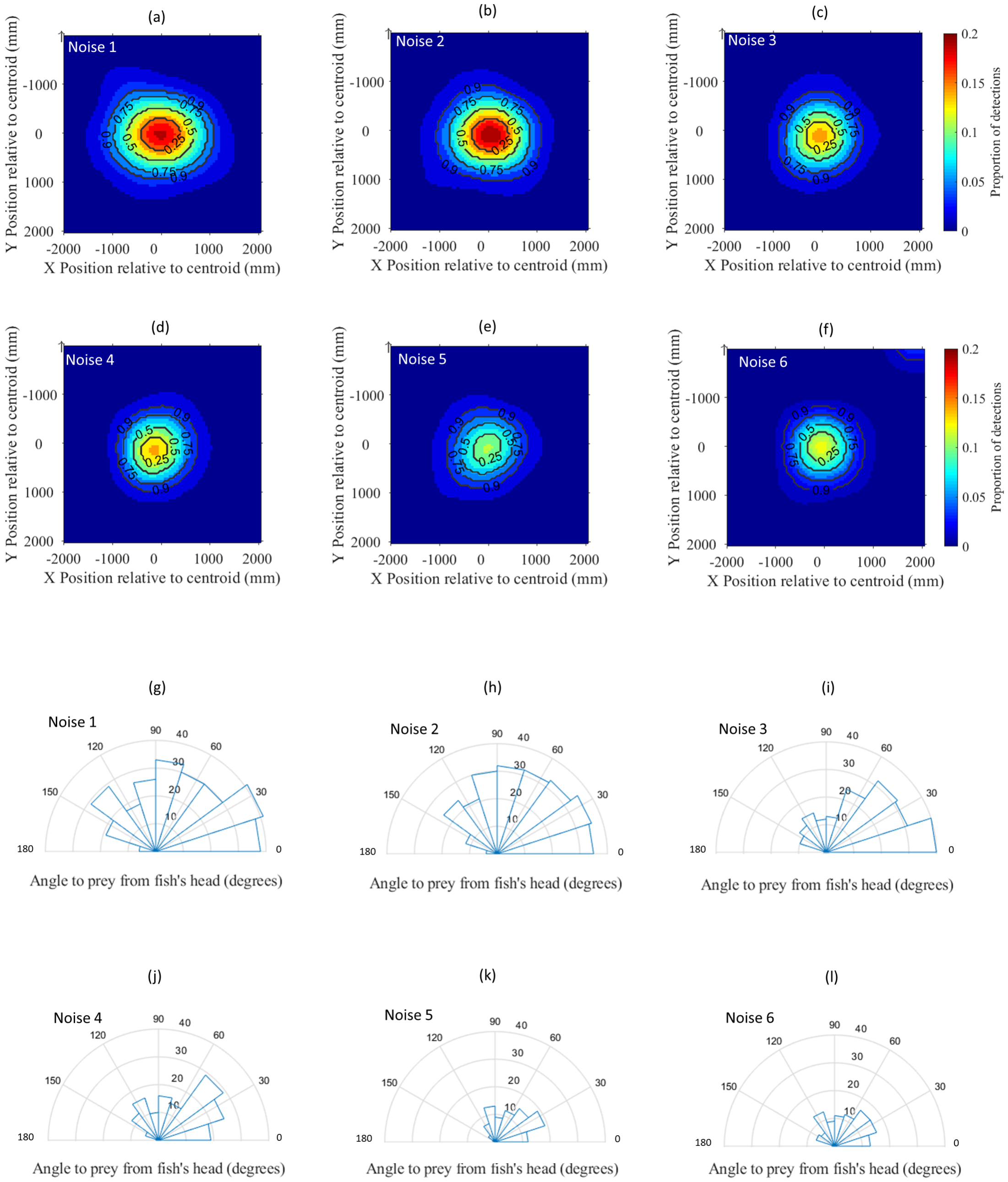


Figure A2.1: Changes in noise affect the likelihood of detection of virtual prey by sticklebacks. a - f) Contour heat plots across all trials. The heat is showing the proportion of responses to the prey divided by the total number of prey presentations in that region with the fish facing along the positive x axis. Hotter colours mean the fish is more likely to detect the prey if it appeared in that position and contour lines are marking the proportions of prey detected within that region, for example 25% of prey are detected within the inner contour marked 0.25. g) - l) Rose plots across all trials showing the angles to the prey when the fish detected the prey. Plots a) and g) are for noise level one, b) and h) are noise level two, c) and i) are noise level three, d) and j) are noise level four, e) and k) are noise level five and f) and l) are noise level six.

CHAPTER 3

FISH AVOID VISUALLY NOISY ENVIRONMENTS

A version of this chapter is published in the following manuscript: Attwell, Joanna R., Ioannou, Christos C., Reid, Chris R., and Herbert-Read, James E. (2021). Fish avoid visually noisy environments where prey targeting is reduced. *American Naturalist* 198(3), 421-432

All organisms' surroundings contain different forms of noise that occur across different sensory domains. In Chapter 2 I demonstrated that a dynamic form of visual noise, caustics, reduced the visual perception of individual sticklebacks. Here I ask whether fish avoid these more visually noisy regions of their environment, thereby avoiding areas where their visual perception may be compromised. Three-spined sticklebacks (*Gasterosteus aculeatus*) were given a choice between associating with a more or less visually noisy area in an experimental choice test. Fish avoided areas of the environment with increased visual noise, and achieved this by increasing their activity as a function of the locally perceived noise level. In a separate experiment, fish did not increase or decrease their refuge use in environments with increased visual noise, providing no evidence that visual noise either increased exploratory or risk aversive behaviour. My results indicate that animals can use simple behavioural strategies to avoid visually noisy environments, thereby mitigating the impacts these environments have on their perceptual abilities.

3.1 Introduction

Background noise is an inherent part of all natural environments, with this noise often making it more difficult for animals to detect or respond to information. Indeed, dynamic visual backgrounds impair the ability of Puerto Rican lizards (*Anolis cristatellus* and *A. gundlachi*) to detect territorial display signals (Ord et al., 2007) and acoustic noise can reduce the foraging success of pallid bats (*Antrozous pallidus*) (Allen et al., 2021). Because noise can reduce the ability of animals to detect or respond to information in their environment, prey and predators may use behavioural strategies to either exploit or avoid noisy regions of their environment. For example, if attempting to remain undetected, some prey species may preferentially select noisier environments, or increase their exploration of the environment during times of increased environmental noise. Indeed, fathead minnows (*Pimephales promelas*), three-spined stickleback (*Gasterosteus aculeatus*), and larval pike (*Esox lucius*), show decreased anti-predator behaviour in more turbid water (Abrahams and Kattenfeld, 1997; Lehtiniemi et al., 2005; Sohel and Lindström, 2015), suggesting they may exploit times of high turbidity to avoid being detected by visual predators (although see (Chamberlain and Ioannou, 2019)). On the other hand, predatory species may attempt to avoid noisier environments as gathering information in those environments becomes more difficult. Some species of bats, for example, avoid areas of their environment with higher levels of acoustic noise (Bennett and Zurcher, 2013) and others spend more time foraging in areas with lower levels of acoustic noise (Schaub et al., 2008) (but see (Bonsen et al., 2015)). When avoidance of noisy areas is impossible, however, some species may adapt their behaviour to compensate for reduced information detection. Zebra finches (*Taeniopygia guttata*), for example, spend more time being vigilant in noisier acoustic environments, but this comes at the cost of decreased foraging rates (Evans et al., 2018).

While animals' behavioural changes to static noise, and in particular acoustic noise, have been relatively well documented (Kunc et al., 2016; Shannon et al., 2016), whether animals adapt their behaviour in response to noise in other sensory channels, and in particular dynamic visual noise, has received far less attention. There is huge natural variation in caustics - their spatial and temporal distribution are dependant on the ambient light levels, water depth, and the speed and size of surface waves. This variation may lead individuals to select habitats based on the environmental noise determined by the local ecological conditions (e.g. Bennett and Zurcher (2013); Schaub et al. (2008)), but whether this habitat choice would represent an adaptive behavioural decision to exploit or avoid noisy environments is unclear. Movement typically breaks camouflage (Ioannou and Krause, 2009), but false motion cues from dynamic noise can mask movement (Bian et al., 2016; Ryerson, 2017). Indeed, false motion cues from caustics can make it more difficult for predators to detect moving prey (Matchette et al., 2020, 2018, 2019). Therefore, exploration during times of increased noise could be less costly for prey, who may therefore exploit these times where this background motion is masking their movement and their likelihood of detection by a predator is reduced. Hence, when in less noisy environments, prey animals may choose to decrease their exploration and increase refuge use during periods when their likelihood of detection by a predator is increased. In contrast, predators may prefer less noisy environments where they are more likely to be able to detect prey.

Many animals like sticklebacks are both predator and prey, so therefore have to search their habitat for food as well as avoid predation risk to themselves. For both predator and prey species, habitat background complexity as well as presence of predators or prey can influence which micro-habitat an individual chooses to associate with (Formanowicz Jr and Bobka, 1989; Kjernsmo and Merilaita, 2012; Kotler et al., 1991). Natural selection should lead predators to select foraging sites that maximise their foraging success (Pyke et al., 1977). One way of doing this could be by selecting habitats that increase prey contrast with the background. Cane toads (*Rhinella marina*), for example, actively select white backgrounds as these provide a greater contrast with their insect prey and this contrast is critical in toad foraging success (González-Bernal et al., 2011). These toads have very few predators in the wild (Lever, 2001) meaning they do not need to trade-off increased foraging success with reducing their own predation risk. However for ambush predators a strategy may be to select habitats with a greater amount of cover. Black Phoebes (*Sayornis nigricans*), for example, choose perches that contain high levels of grass and tree cover and are at a low light intensity when waiting to ambush prey. This could be to increase capture success as well as to reduce predation risk to themselves (Gall and Fernández-Juricic, 2009). Prey animals should choose to associate with habitats that match their own body colours and patterns in order to conceal themselves (Cott, 1940). It has been shown experimentally in many fishes that background matching can reduce predation risk (Feltmate and Williams, 1989; Johnsson and Kjällman-Eriksson, 2008). Refuge use is another strategy that prey animals can use to provide cover from predators, but this comes with a trade-off in how long to spend under cover verses foraging outside of cover. The longer an individual stays hidden in a refuge, the more likely they are to avoid predation, but this comes with an energetic cost due to lost foraging opportunities (Krause et al., 1998). One study that demonstrates this trade-off found that barnacles hide longer from a predatory stimulus after having spent more time feeding prior to this, with barnacles that have an increased starvation time hiding for less time (Dill and Gillett, 1991). Hunger state can therefore shift the costs and benefits of refuge use compared to foraging. Therefore animals should select habitats that maximise the trade-off between increased foraging success while also reducing the predation risk.

Here I asked whether three-spined sticklebacks (*Gasterosteus aculeatus*) select or avoid areas of their environment with increased visual noise and asked how visual noise affects their refuge use. To understand whether sticklebacks, exploit or avoid these visually noisy areas, I performed two experiments. I first asked whether sticklebacks avoided or spent more time in areas of the environment with increased levels of visual noise. In this experiment, I also determined whether fish were actively or passively avoiding areas of the environment with different levels of visual noise. I did this by quantifying their activity (speed and time spent stationary) in response to the locally perceived level of noise, and by asking whether there was directed movement towards or away from noisier areas. I then tested whether the fish increased or decreased refuge use in different levels of visual noise, using this as an indication of whether the fish chose to explore their environment when their own likelihood of being detected was lower.

3.2 Methods

3.2.1 Study subjects and experimental arena

Three-spined sticklebacks were caught from the river Cary in Somerton, Somerset, UK (51.069990 latitude, -2.758014 longitude), and I observed caustics in the location that the fish were caught. Fish used in experiment one were caught in November 2017, and fish used in experiment two were caught in March 2019. All fish were housed for at least two weeks before experimentation in the same way and under the same conditions as in Chapter 2.

The experimental tank for both experiments was also the same as that used in the previous chapter, consisting of a test arena (1.46 x 0.84 m, length x width) and a holding area (0.84 x 0.34 m, length x width) separated by white opaque plastic (Chapter 2: Figure 2.2). Fish again were left to acclimate in the holding area for the night prior to their trial and were not fed for 24 hours before the experiment. The same camera and projector as those used in the Chapter 2 were used and operated in the same way.

3.2.2 Choice experiment

Playbacks of simulated caustics of six different speeds were projected into the arena as in the previous chapter, however in these projections no virtual prey were presented. To determine if fish avoided or preferred to associate with more or less visually noisy environments, individual fish were presented with a binary choice, where on one side of the arena I projected one level of visual noise, and on the other side I projected a different level of visual noise. As there were six different levels of noise, this gave 15 possible combinations of noise pairings. I constructed six different playbacks, where each playback contained all 15 different noise pairings, played one after the other. Each choice (noise pairing) was presented for 320 seconds, with the total length of each playback equalling 80 minutes. Across the different playbacks (n = 6), each noise level was presented evenly on each side of the test arena to control for any potential side biases. The ordering of the noise pairings within a playback were also assorted between the six playbacks so there was no systematic bias in their ordering across the trials (Table 3.1). For each trial, a single fish was exposed to one of these six playbacks. The order of the six playbacks was randomised within each day, with each playback being used a maximum of once per day.

Table 3.1: Order that the different levels of noise were presented within each playback for the choice experiment. The letter above each pair of columns is the name of the playback.

Order within trial	**a**		**b**		**c**		**d**		**e**		**f**	
	Left	**Right**	**Left**	**Right**	**Left**	**Right**	**Left**	**Right**	**Left**	**Right**	**Left**	**Right**
1	5	1	3	2	2	1	2	4	4	3	5	2
2	4	3	1	4	6	4	6	1	2	6	3	6
3	6	2	6	5	3	5	5	3	5	1	4	1
4	1	2	1	5	5	6	2	5	5	6	6	5
5	3	5	6	2	1	4	6	3	4	2	2	4
6	4	6	3	4	2	3	1	4	3	1	3	1
7	3	6	1	6	1	3	6	4	3	5	3	2
8	5	2	2	4	6	2	3	2	1	2	5	4
9	4	1	5	3	4	5	1	5	4	6	6	1
10	4	2	5	2	4	3	6	5	4	1	3	4
11	3	1	6	4	2	5	3	4	2	5	2	6
12	5	6	1	3	1	6	2	1	6	3	1	5
13	4	5	3	6	4	2	5	4	5	4	4	6
14	2	3	4	5	6	3	2	6	6	1	5	3
15	1	6	2	1	5	1	1	3	2	3	1	2

For each trial (n = 48), an individual fish (5.4 cm ± 0.7 cm, mean ± SD) was moved from the holding area into the test arena and left to acclimate there for 10 minutes. During this period, the first frame of the playback was projected into the test arena as a static image, but the video playback was not started. After ten minutes, I started the video playback remotely. After each trial, the fish was removed and placed in a separate housing tank and fed. No fish were reused between trials.

Fish were tracked using an adapted version of DIDSON tracking software (Handegard and Williams, 2008) in MATLAB 2018a (MATLAB, 2018) (Figure 3.1). Because the fish were darker than the arena or moving projections, I took a grey-scale threshold of each frame to isolate the fish within the videos without requiring any background subtraction. X and y coordinates of the fish were smoothed using a rolling average of 12 frames (approximately half a second). Tracks were only smoothed if at least 50% of the tracks were present within these 12 frames (using the function *nanfastsmooth* in MATLAB), otherwise these segments of the tracks were removed (replaced with NaN). Smoothing is a standard procedure used in trajectory analysis, allowing spurious errors in point estimates to be reduced (Calenge et al., 2009; Gautrais et al., 2012; Herbert-Read et al., 2011; Katz et al., 2011; MacGregor et al., 2020; Pérez-Escudero et al., 2014; Spitzen et al., 2013; Tunstrøm et al., 2013) and I provide a visualisation of this smoothing (Figure 3.2). In addition to plotting and manually inspecting the tracks for accuracy, I calculated that fish were tracked for 88.2% of all frames (see below). The tracking accuracy was not systematically affected by different levels of visual noise (see Figure 3.3 and section 3.2.3). Nor was there a difference in the tracking accuracy between different sides of the arena (Figure 3.3, Figure 3.4).

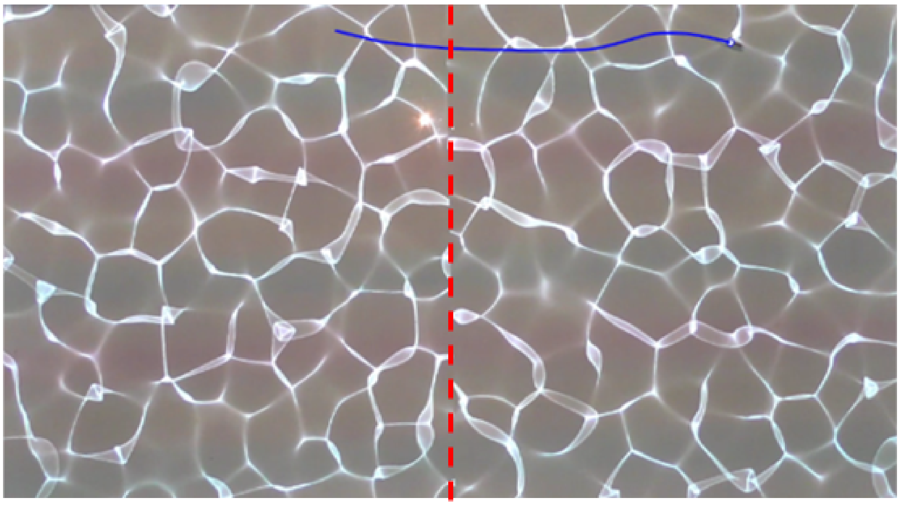


Figure 3.1: Experimental arena and choice test in Experiment 1. A still image from a video of a choice trial depicting a section of the trajectory of a fish superimposed in blue. The red dashed line shows the virtual boundary between the two choice areas on the left and right hand side.

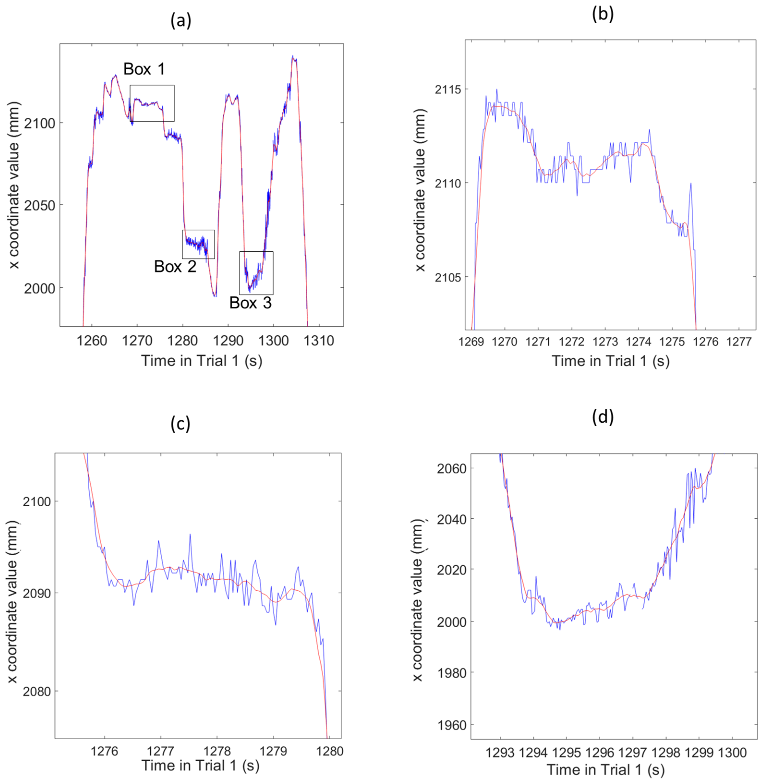


Figure 3.2: Visualisations of the smoothing procedure for an example trial. In all plots, smoothed x coordinates (in red) are plotted over the original x coordinates (blue). a) 50 seconds worth of x coordinates from one of the trials (Trial 1), with boxes indicating regions of interest featured in subsequent subplots b) box 1, c) box 2, d) box 3.

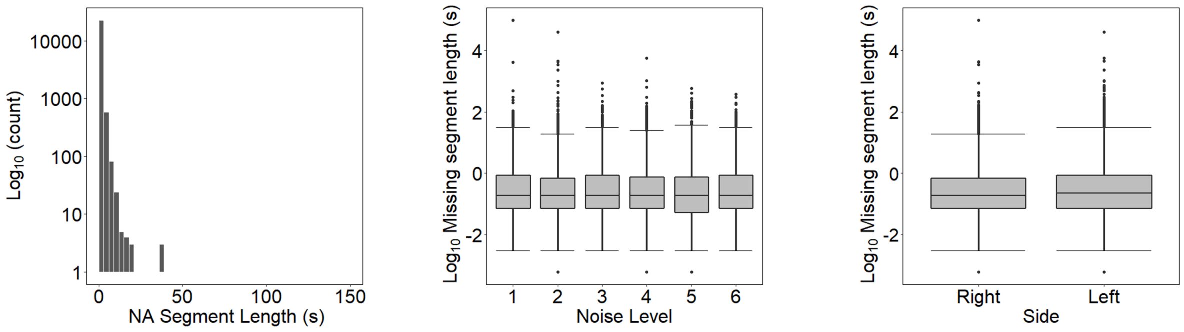


Figure 3.3: Measures of tracking accuracy. a) Histogram of the number of continuous frames where the fish were not tracked (NaN segments) within all trials. Note the majority of missing tracks were missing for less than 1 second and the log scale on the y axis. b) Log missing segment length as a function of noise level. c) Log missing segment length for the right and left side of the arena. The central line of each box shows the median value while the upper and lower lines of the box show the upper and lower quartiles of the data, with the whiskers extending to the most extreme data point within 1.5 × the interquartile range. Jittered dots represent raw data points.

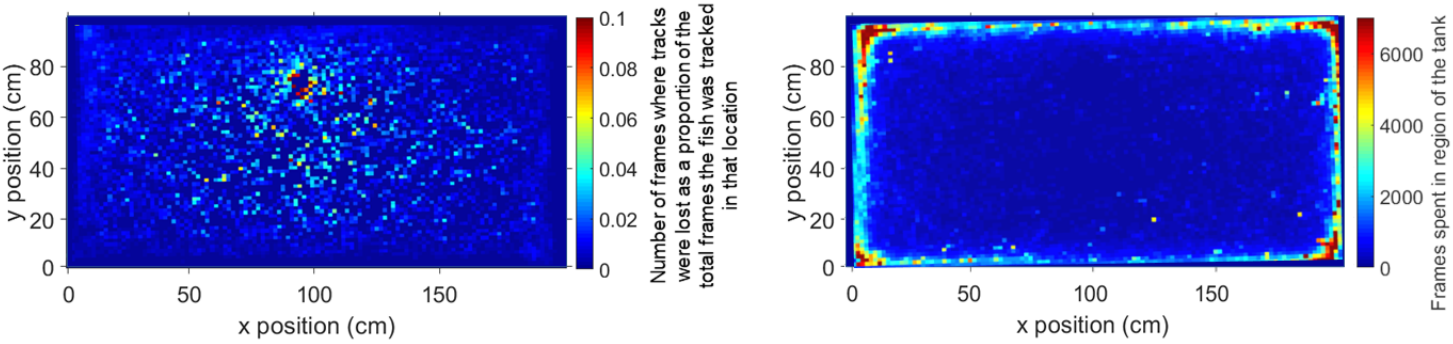


Figure 3.4: a) Locations in the arena where tracks were lost as a proportion of the number of frames that the fish was tracked in that location. Hotter regions indicate regions where this happened most frequently. The central region at 100 x, 80 y, is where the reflection from the projector lamp impeded tracking. Generally, however, tracking errors appeared randomly distributed in the tank and there was no difference in tracking accuracy between the left and right sides of the arena (see Fig. A3) b) Heatmap of the positions that the fish were located in the arena (in 1 x 1 cm bins). Positions of the fish were extracted every second within all trials. Hotter regions indicate where the fish spent more time, which was generally around the edges and corners of the arena.

From the trajectories of each fish, I calculated the amount of time the fish spent on each side of the test arena in each paired choice. To do this, I used the *inpolygon* function in MATLAB 2018a (MATLAB, 2018) to determine when a fish's track was either on the left or right side of the arena. I then calculated the proportion of time that the fish spent in the noisier side of the arena for each noise pairing.

To gain an understanding of how fish were selecting to associate with areas with different levels of noise, I assessed how their movement adapted in the different noise levels. The proportion of time that the fish spent in different levels of noise could result from fish adopting different movements as a function of the noise level they were in, and potentially the noise level on the other side of the arena. For example, if the fish adopted different speeds, or spent less time moving, this could result in the fish spending unequal amounts of time in each level of noise. To assess this I first calculated the amount of time the fish spent stationary, and the speed they adopted when they were moving, when in different levels of noise. To do this, the instantaneous speed of the fish was calculated as the displacement in their position between two consecutive frames. I defined a fish as being stationary when its speed was less than 2 mm s^{-1}, informed by plotting a histogram of all the fish's speeds across all trials (Figure 3.5). The mean speed of a fish was calculated excluding the times when they were stationary (i.e. when speeds were > 2 mm s^{-1}), and was calculated when the fish was on each side of the arena separately. I also tested whether the fish showed any evidence of directed movement towards or away from the sides of the arena with more or less visual noise, which would be indicative of the fish making an active choice to avoid those areas. To do this, I calculated the proportion of time the fish spent facing towards the opposite side of the arena to that which it was on within each choice by calculating the proportion of time in each noise treatment that they spent facing left and right and the proportion of time they spent in each side of the arena. I predicted that if the fish were making an active choice, they would spend greater than 50% of their time facing the less noisy side when on the noisier side of the arena, and spend less than 50% of their time facing away from the visually noisier side when on the less noisy side of the arena.

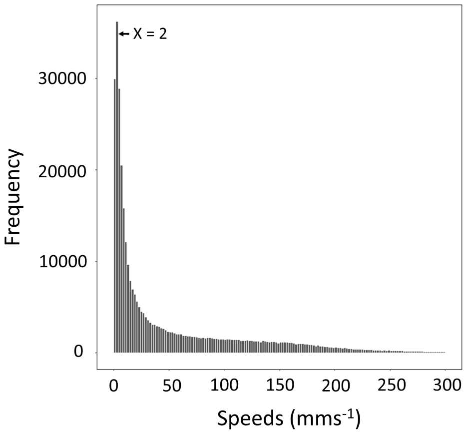


Figure 3.5: Distribution of all fish's instantaneous swim speeds across all choice experiment trials. The line marked at X = 2 is to indicate the cut off, below which the fish was classified as being stationary.

3.2.3 Tracking accuracy in different levels of noise

To ensure the tracking accuracy was not systematically affected by the level of visual noise in the choice experiment, I calculated the lengths of continuous tracked segments (i.e. unbroken periods when the fish were tracked) in each level of visual noise (Figure 3.3 a). I then tested whether the tracked segment length changed as a function of noise level using a linear mixed model (LMM). The segment length was log transformed due to a strong positive skew. The segment lengths for each side of the arena, per choice, per trial, were given a unique ID (for each trial there were 15 paired noise choices, meaning each trial had up to 30 unique IDs). This meant that all tracked segment lengths within each choice could be grouped together and accounted for by a random factor in the model. Noise level was added as the explanatory variable and the unique ID within trial was added as a random intercept. The median tracked segment length was found to be 3 seconds (IQR = 7.32) and the mean was 7.48 seconds (SD = 14.76). Although these tracked segment lengths are short, the average tracking accuracy across all trials and noise levels was 88.2%, hence tracked segments were only broken for relatively short periods of time. Noise level did not affect the length of the tracked segments, and hence would not have affected the interpretation of my results (Figure 3.3b) LMM; Estimate = $1.01, \chi^2 = 1.78, df = 5, p = 0.18$).

3.2.4 Refuge experiment

To determine whether the fish were more or less likely to use a refuge in different levels of visual noise, two plastic plants (each 5 x 2 x 15 cm, length x width x height) were placed as a refuge in the middle of the test arena (Figure 3.6). For each trial (n = 48), an individual fish (4 ± 0.5 cm; mean ± SD) was exposed to six different levels of visual noise, with each level of noise being projected throughout the entire arena, and each level of noise projected sequentially one after the other. To ensure that each noise level was presented in a different order within trials, I again created six playbacks where each playback contained each level of noise, but each noise level occurred in a different order within each playback (referred to as order-within-trial) in a Latin-square design (Table 3.2). Each trial, therefore, consisted of six levels of noise, each presented for 320 seconds, with the total running length of the playbacks equalling 32 minutes. Every playback was presented exactly once per day and in a random order each day (between 9am and 5pm) on different days. As in the choice tests, individual fish were moved from the holding area and placed in the test arena for 10 minutes acclimation time (while a static caustic image was projected into the arena) before the playback was started remotely. Experimented fish were removed and placed in a separate housing tank and fed. They were kept separately from unused fish and fish were not reused between trials. Fish that were used in the refuge experiment had not been used in the choice experiment.

Table 3.2: Order that the different levels of noise were presented within each playback for the refuge experiments. The letter above each of the columns is the name of the playback. One playback was given to each fish and each noise level occurred at all different times in the six playbacks in a latin square design.

Order within trial	**Playback**					
	a	**b**	**c**	**d**	**e**	**f**
1	2	3	1	6	4	5
2	4	1	5	2	6	3
3	1	5	4	3	2	6
4	6	4	3	1	5	2
5	3	6	2	5	1	4
6	5	2	6	4	3	1

I scored the amount of time (in seconds) the fish spent under the refuge during each level of noise. To do this, videos were imported into the software BORIS v. 7.9.15 (Friard and Gamba, 2016), where I defined the fish to be under the refuge when any part of its body was under any of the fronds of the plastic plant (see Figure 3.6). Each fish could therefore be under the refuge for a minimum of 0 to a maximum of 320 seconds in each level of visual noise.

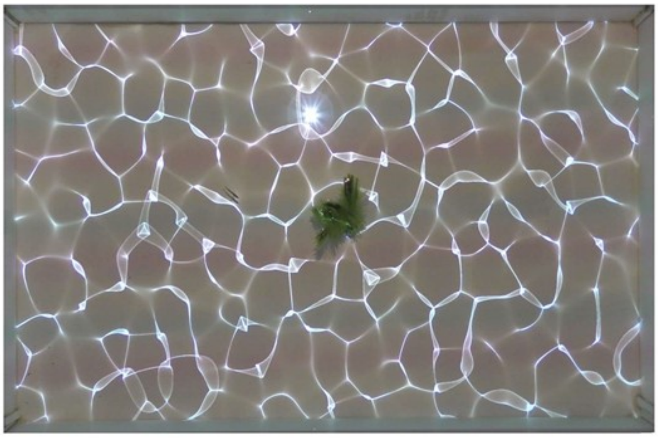


Figure 3.6: Setup of the refuge experiment (Experiment 2) with two plastic plants located next to each other in the middle of the arena. The size of each of the plants measured 5 x 2 x 15 cm (length x width x height), but as seen from the image, the fronds of the plastic splayed out when submerged. A focal fish (for size comparison) can be seen to the left of the refuge, midway between the upper and lower sides of the arena.

3.2.5 Statistics

All statistics were performed in R 3.5.1 (R Core Team, Version 3.5.1). The package lme4 (Bates et al., 2015) was used for all mixed models. Assumptions for all linear mixed models (LMMs) were checked using standard diagnostic plots (QQ normal plots and residuals plotted against fitted values). Models were also checked for collinearity. Assumptions for all generalised linear mixed models (GLMMs) were checked using the DHARMa package (Hartig, 2019) including checking the dispersion and the distribution of the residuals. The full models were simplified by removal of non-significant terms. I used the *anova* function in R (R Core Team, Version 3.5.1) to compare pairs of models using the chi-squared statistic. All R graphs were created using *ggplot2* (Wickham, 2016).

Choice experiment – To test whether fish spent more or less time in areas with more or less visual noise (regardless of absolute noise level), I subtracted 0.5 from the proportion of time they spent on the noisier side of the arena separately for each choice of the 15 noise pairings per trial. I tested whether the intercept of a linear mixed model (LMM) predicting those proportions, with trial included as a random effect, differed from zero (i.e. proportion of time on the noisier side - 0.5 ~ 1 + (1 | Trial) in *lme4* nomenclature). I then asked whether the absolute difference in noise level within a choice affected the amount of time the fish spent on the noisier side of the arena. To do this, I calculated the difference between noise levels on each side of the arena for each noise pairing. For example, the difference between a choice of noise levels one and five was calculated as four. I then used a LMM to ask whether this difference could predict the proportion of time the fish spent on the noisier side of the arena. In this model, the difference in noise was treated as a discrete numeric variable, trial (fish identity) was included as a random intercept, and difference in noise level was included as a random slope.

I used LMMs to predict whether a fish's speed, and in a separate model the time spent stationary, on the side of the arena the fish was in could be predicted based on the level of noise on each side of the arena (modelled as separate fixed effects: noise level on the side occupied by the fish and noise level on the unoccupied side). Mean speed and the proportion of time stationary were square root transformed due to a slight positive skew of these data. Order-within-trial (1-6) was also added as a fixed effect and trial was included as a random intercept along with noise level on the side occupied by the fish as a random slope.

Because a fish's speed, and time spent stationary, were dependent on the noise level they were in (but not dependent on the noise level on the other side of the arena – see below), I asked whether the differences observed in speed and time spent stationary could solely explain the amount of time fish spent in the corresponding levels of visual noise. To do this, the mean speed that the fish adopted in different levels of noise, along with the proportion of time spent stationary, were added as covariates into the model investigating proportion of time spent on the side of the arena with more visual noise.

To test if the fish were showing directed movement towards one side of the tank and therefore making an active choice, I used two separate linear mixed models with i) the proportion of time facing the less noisy side of the tank (when the fish was on the noisier side of the arena) or ii) the proportion of time facing the noisier side of the arena (when the fish was on the less noisy side) as the response variables. Due to the heavy tails of both these response variables, I used the LambertW (Goerg, 2015, 2020) package in R to transform the data to a gaussian distribution. To do this, I first used the *MLE_Lambert* function to estimate the parameters of the distribution and then back-transformed the data using the *get_input* function. I then subtracted 0.5 from each of the response variables and tested whether the intercept of the models differed from 0. Noise on the noisier side of the arena and noise on the less noisy side of the arena were added as fixed effects and trial (fish identity) was added as a random intercept to the models.

Refuge experiment - I tested if the level of visual noise had a significant influence on the time the fish spent under refuge. I initially attempted to model the proportion of time spent under refuge as a function of the level of noise using a LMM, but the models failed to converge. Therefore, I transformed the response variable (time spent in refuge) into a binary response variable (Figure 3.10a), where fish that spent over 50% of their time in the refuge were given a value of 1, and less than or equal to 50% a value of 0. This binary response variable was modelled using a GLMM with a binomial error structure. Noise level was included as a fixed effect (discrete numeric as before) along with order-within-trial, and trial (fish identity) added as a random effect. I did not include noise as a random slope in the refuge experiment because there was no effect of noise on the response variable.

3.3 Results

3.3.1 Choice experiment

Fish spent more time on the side of the arena with less visual noise (Figure 3.7a) (LMM; $t_{47} = -7.8, p < 0.001$). Furthermore, the relative difference between the noise levels on each side of the arena affected the time the fish spent in the noisier side of the arena. As the relative difference in noise between the two sides of the arena increased, fish spent less time on the side of arena with more visual noise ((Figure 3.7b); LMM; $\chi^2 = 7.79, df = 7, p = 0.005$; for 95% confidence intervals see Table 3.3). When repeating this analysis and only including cases where the fish visited both sides of the arena, the results did not qualitatively change. Fish again spent more time on the side of the arena with less visual noise (LMM; $t_{45} = 8.4, p < 0.001$) and as the relative difference in noise between the two sides of the arena increased, fish spent less time on the side of arena with more visual noise (LMM; $\chi^2 = 7.79, df = 7, p = 0.005$).

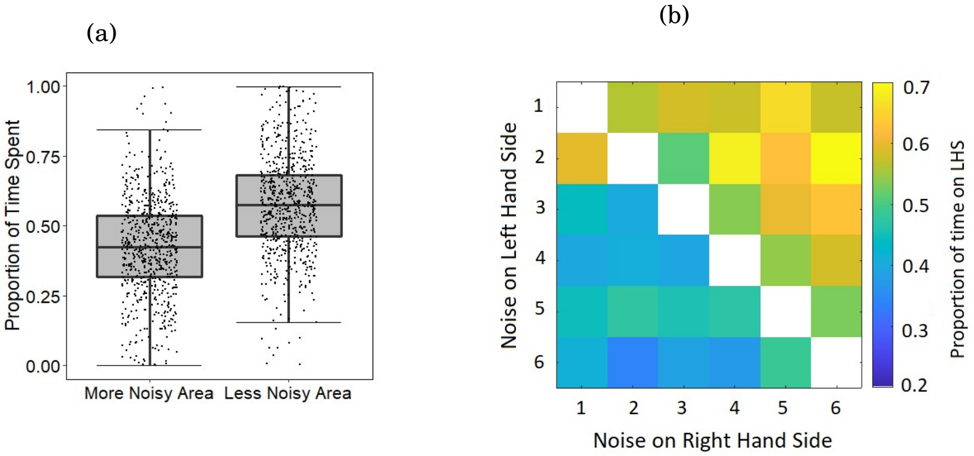


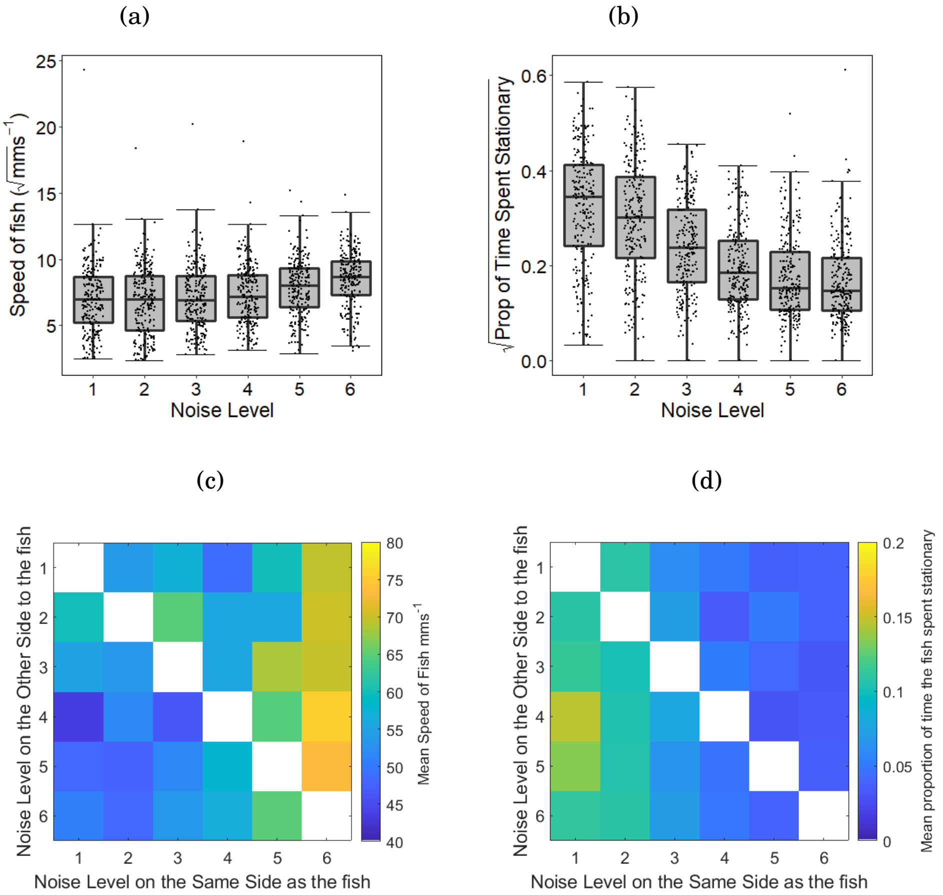
Figure 3.7: Choice test. a) Proportion of time the fish spent on the side of the arena with more or less visual noise (ignoring absolute differences in noise level). Fish spend more time on the side of the arena with less visual noise. The central line of each box shows the median value while the upper and lower lines of the box show the upper and lower quartiles of the data, with the whiskers extending to the most extreme data point within 1.5 × the interquartile range. Jittered dots represent raw data points. b) Matrix showing the proportion of time (the heat) the fish spent on the left side of the arena where each cell represents the choice a fish was given between two levels of visual noise. Six represents the highest level of noise, and one the lowest. When the noise level was *lower* on the left side of the arena (upper-right corner of the plot), the fish spent *more* time on that side. When the noise level was *higher* on the left side of the arena (lower-left corner of the plot), the fish spent *less* time on that side. Note that 1 minus this matrix would give the proportion of time spent on the right hand side of the arena.

Table 3.3: Mean values of the proportion of time spent on the left-hand side of the arena (as in Fig 3.7b) including the bootstrapped 95% confidence intervals in brackets.

		Noise on the right-hand side					
	Noise level	1	2	3	4	5	6
Noise on the left-hand side	1	NaN	0.56 (0.49, 0.63)	0.58 (0.50, 0.67)	0.58 (0.49, 0.66)	0.66 (0.58, 0.74)	0.57 (0.50, 0.64)
	2	0.59 (0.49, 0.71)	NaN	0.51 (0.45, 0.57)	0.69 (0.58, 0.79)	0.62 (0.55, 0.70)	0.70 (0.62, 0.78)
	3	0.44 (0.39, 0.50)	0.40 (0.28, 0.52)	NaN	0.54 (0.47, 0.61)	0.60 (0.52, 0.67)	0.63 (0.55, 0.71)
	4	0.40 (0.32, 0.47)	0.41 (0.32, 0.49)	0.39 (0.31, 0.48)	NaN	0.54 (0.49, 0.59)	0.58 (0.51, 0.64)
	5	0.45 (0.33, 0.57)	0.48 (0.39, 0.57)	0.46 (0.39, 0.54)	0.47 (0.40, 0.55)	NaN	0.53 (0.48, 0.59)
	6	0.41 (0.30, 0.53)	0.34 (0.27, 0.43)	0.39 (0.30, 0.47)	0.37 (0.30, 0.45)	0.49 (0.43, 0.55)	NaN

The fish's movements were only affected by the level of visual noise on the side of the arena they were in. Fish moved faster (Figure 3.8a; LMM; $\chi^2 = 52.3, df = 8, p < 0.001,$) and spent less time stationary (Figure 3.8b; LMM; $\chi^2 = 90.8; df = 8, p < 0.001$) when on the side of the arena with more visual noise. The noise level on the other side of the arena (to that which the fish was on) did not affect the fish's speed (Figure 3.8c; LMM; $\chi^2 = 0.35, df = 8, p = 0.55$), nor the proportion of time it spent stationary (Figure 3.8d; LMM; $\chi^2 = 0.34, df = 8, p = 0.56$). When these movement variables were added as covariates to the model, the difference in noise level between the two sides of the arena was no longer a significant predictor of the time the fish spent on the noisier side (LMM; $\chi^2 = 1.61, df = 11, p = 0.20$). The fish's speed and its time spent stationary on the noisier side of the arena, therefore, could explain the proportion of the time spent on that side of the arena. In other words, how a fish adapted its movements to the locally perceived level of noise determined the amount of time it spent in that region.

There was no evidence that the fish were making an active choice to move away from noisier areas of the environment. When on the less noisy side of the arena, fish were not more likely to face towards or away from the noisier side (Figure 3.9a; LMM; $t_{512} = 1.54, p = 0.125$). When on the noisier side of the arena, fish were also not more likely to face towards or away from the less noisy side (Figure 3.9b; LMM; $t_{568} = 0.52, p = 0.60$).



(a) (b)

(c) (d)

Figure 3.8: How the fish's movements were affected by visual noise in the choice experiment. a) Square root of fish's mean speed as a function of the visual noise level they were in. Fish swam faster in more noisy areas. b) Square root of the proportion of time the fish spent stationary as a function of the noise level they were in. Fish spent less time stationary in more noisy areas. In a) and b) the central line of each box shows the median value while the upper and lower lines of the box show the upper and lower quartiles of the data. The whiskers extend to the most extreme data point within 1.5 × the interquartile range. Outliers are shown by the larger grey circles. Jittered points represent raw data points. c) Mean speed of fish (the heat) as a function of the noise level the fish was in (columns) and the noise level on the other side of the arena (rows). d) Mean proportion of time the fish spent stationary as a function of the noise level the fish was in (columns) and the noise level on the other side of the arena (rows). One – six corresponds to the lowest – highest levels of noise respectively. The presence of a trend from left to right, but not top to bottom, in these heat plots indicates that the fish moved faster, and spent less time stationary, in higher levels of visual noise, but the noise level on the other side of the arena did not affect their movements.

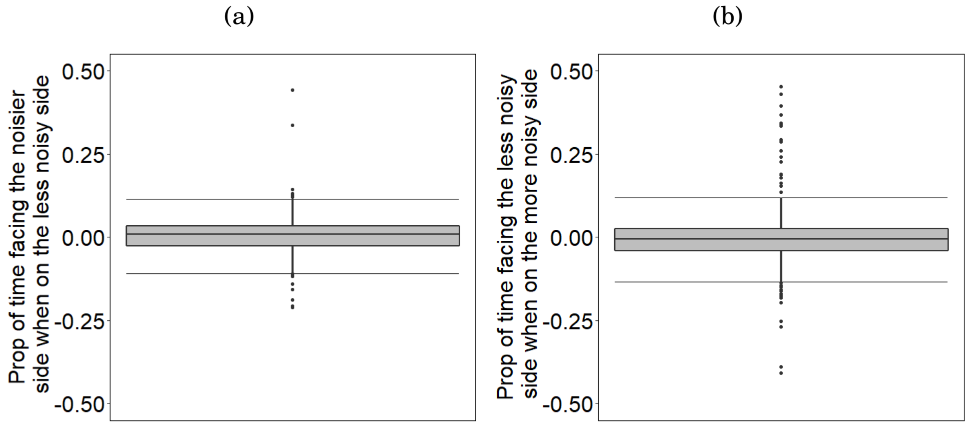


Figure 3.9: The proportion of time the fish spent facing towards or away from the noisier side of the arena within the choice tests. a) The proportion of time the fish spent facing the noisier side of the arena when on the less noisy side, minus 0.5. b) The proportion of time the fish spent facing the less noisy side of the arena when on the noisier side, minus 0.5. The central line of each box shows the median value while the upper and lower lines of the box show the upper and lower quartiles of the data, with whiskers extending to the upper and lower values 1.5 × the interquartile range.

3.3.2 Refuge experiment

There was no evidence that the level of visual noise affected whether the fish spent the majority of time under the refuge or not (Figure 3.10b; GLMM; $\chi^2 = 3.27, df = 4, p = 0.071$). However, fish did spend less time under the refuge as the trial progressed (GLMM; $\chi^2 = 12.1, df = 4, p < 0.001$).

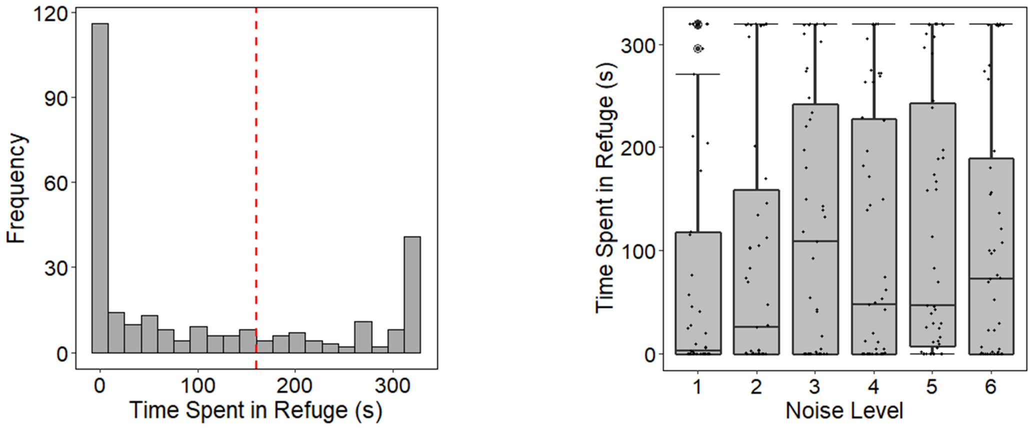


Figure 3.10: Refuge experiment a) Distribution of the time the fish spent in the refuge (max 320 seconds) for all levels of noise across all experiment trials. The red dashed line at x = 160 indicates the cut off below which I classified fish as spending the majority of time out of the refuge (0), or above which I classified the fish as spending the majority of time in the refuge (1). b) Amount of time the fish spent in the refuge as a function of noise level (however, note this was analysed using a binomial GLMM as defined in a)). The time spent in the refuge was not affected by the noise level. The central line of each box shows the median value while the upper and lower lines of the box show the upper and lower quartiles of the data, with whiskers extending to the upper and lower values 1.5 × the interquartile range. Jittered points represent raw data points.

Table 3.4: Estimates and Cohen's D for each of the statistical tests

Explanatory Variable	**Main Response variable**	**Estimate**	**Cohen D**
Choice Experiment			
Proportion time noisy side -0.5	*Intercept model*	-0.08	NA
Proportion time noisy side	Noise difference	-0.02	2.14
Fish swim speed	Noise on side of fish	0.09	1.88
Fish proportion of time stationary	Noise on side of fish	-0.001	-2.70
Fish swim speed	Noise other side to fish	-0.0002	1.86
Fish proportion of time stationary	Noise other side to fish	-0.001	-2.73
Proportion time noisy side	Noise difference, Swim speed, Prop. of time stationary	0.0066	3.31
Refuge Experiment			
Time in refuge	Noise level	0.17	2.49
Time in refuge	Order-within-trial	-0.32	2.49

3.4 Discussion

Fish spent less time in areas with more visual noise, and this reduction in time could be attributed to how the fish adapted their movements in response to noise. In particular, fish increased their speed and spent less time stationary in areas with more visual noise. There was no evidence, however, that the level of visual noise on the other side of the arena affected their movements, nor that fish directed their movement towards less noisy areas, suggesting that the fish were only responding to the level of noise in their local vicinity. While increases in speed and decreases in time spent stationary could be interpreted as the fish exploiting noisy environments to increase exploration during times of increased environmental noise, my second experiment provided evidence against this explanation. If fish were exploiting times of higher visual noise to avoid themselves being detected, I would have expected the fish to spend less time in the refuge in higher levels of visual noise (as refuge use is a key measure of risk taking in sticklebacks (Bevan et al., 2018)). In fact, I found no evidence that fish altered their risk-taking behaviour depending on noise level. Further, it is unlikely that fish were increasing their activity in noisier areas to match their swim speed with the movements of the caustics, as the optical flow produced by the caustics did not move in a consistent direction (see Figure 2.1a). Instead, I suggest that fish use a simple mechanism, namely increasing their speed and activity, to avoid areas of their environment with higher levels of visual noise.

Increasing activity in unfavourable regions of the environment to avoid those areas is a mechanism termed ‘orthokinesis’, first defined by Fraenkel and Gunn (1961). This occurs when an animal’s movements change depending on the intensity of a localised environment stimulus. Fraenkel and Gunn (1961) found that woodlice move faster in areas of low compared to high humidity, leading to the woodlice spending more time in humid areas. Similarly, the estuarine fish *Micropogon undulates* moves faster in environments with changing salinity as compared to environments with a fixed salinity, leading them to aggregate in areas of fixed salinity (Perez, 1969). Similar mechanisms have been proposed for how groups of animals collectively track resources in their environment (Berdahl et al., 2013; Hein et al., 2015). In my case, this mechanism could lead fish to passively move out of areas with more visual noise and towards regions of the environment with lower visual noise. This could provide a simple, yet effective mechanism to move towards or away from particular regions of the environment without detecting where more favourable regions of the environment are located.

The results in Chapter 2 provide support that these visually noisy environments should be avoided by sticklebacks, with increased visual noise reducing their ability to detect prey. Fish were less likely to detect the virtual prey in these environments, consistent with other systems where humans, chicks and triggerfish took longer to detect prey on backgrounds with dynamic visual noise as opposed to static controls (Matchette et al., 2018, 2019). Because animals have finite time and energy reserves, and limited attention (Cuthill et al., 2019), they are expected to make optimal foraging decisions that increase the rate or efficiency at which they gather resources (Schoener, 1971; Stephens and Krebs, 1986; Ydenberg et al., 1994). This allows them to devote more time and energy to other fitness-related activities (Pianka, 1988; Schmid-Hempel, 1991). Much like how animals choose foraging patches based on their profitability (Krebs, 1979; Milinski, 1979, 1987), I might expect animals to selectively choose where to forage in their environment based not only on the resource profitability of a patch, but also considering the likelihood of detecting those resources given the perceptual constraints imposed by that environment. In Chapter 2, I suggest that the increased activity of the fish could be to increase encounter rates with prey in perceptually demanding conditions. Instead, based on the results in this chapter, I suggest that this could be due to the fish trying to avoid these noisy areas where prey detection is reduced. Indeed, there is large natural variation in both the temporal and spatial distribution of caustics in the aquatic environment, as well other forms of environmental noise. Such variation may lead foragers to select habitats based on the environmental noise determined by the local ecological conditions (e.g. Bennett and Zurcher (2013); Schaub et al. (2008)).

While fish avoided visually noisier environments, these behavioural responses to environmental visual noise may vary as a function of other factors such as hunger state, habitat type or predation. For example, sticklebacks have been shown to both decrease (Sohel and Lindström, 2015) or increase (Ajemian et al., 2015; Chamberlain and Ioannou, 2019) their anti-predator behaviour and refuge use in more turbid water (a form of static visual noise). This suggests their response to visual noise could vary depending on context or state. Indeed, fifteen-spined stickleback (*Spinachia spinachia*), are less risk averse when hungry, but when partially satiated, choose less productive areas where they can spend more time being vigilant (Croy and Hughes, 1991). In my experiments, I did not feed the fish for 24 hours prior to the experiments to induce exploratory behaviour. This may have resulted in the fish attempting to avoid noisier areas to forage more efficiently and this preference could then have shifted the costs and benefits of foraging out of cover in different levels of noise. This would mean that the fish should be more willing to leave the refuge in lower noise levels and forage despite the risk to themselves if their foraging success is likely to be higher. It would also be valuable, therefore, to test if the fish also avoid visually noisy environments when they are satiated, or when the level of risk in the environment is greater. Indeed, I might expect animals to choose noisier areas of the environment when satiated or when faced with greater risk.

Other next steps in this research could include looking at behavioural responses to long term noise exposure when individuals do not have the option to avoid noisy areas. Furthermore, it would be valuable to test if these behavioural changes that fish show are adaptive. More specifically whether these changes in the fish's exploration and changes in motion search strategy (Chapter 2) lead to a greater increase in prey detection in higher levels of noise than would otherwise be achieved. Simulation studies that can manipulate the movements of individuals in different noise levels based on experimental data could provide steps to help answer this question.

In summary, my results demonstrate that individuals can use simple behavioural strategies to avoid visually noisy environments which could be an adaptive response to mitigate the impacts these environments have on their perception. Individuals can increase their activity in more noisy areas leading to them moving out of these areas more quickly and into less noisy areas. This could lead to an increased likelihood of gathering information, and thereby compensate for the potential negative impacts of environmental noise on their perception.

CHAPTER 4

SOCIAL RESPONSES TO NOISE

Environmental noise can reduce the ability of animals to gather information from their environment. In response, group-living animals may be able to adapt their social behaviour to mitigate some of these impacts of noise on their perceptual abilities. For example, individuals in groups may divide information gathering between group members or rely more on social information under noisy conditions. For animals that coordinate their movement in groups, measures such as polarisation, bearing angles, and separation distances provide information about where different individuals are gathering information from in their environment. Further, by assessing whether the speed and directional changes of neighbours are copied by others, this can give insight into how information is transferred between group members. Here I ask whether pairs of fish can compensate for some of the reduction in perception in noisy conditions by distributing search between one another and by using social information. Fish did not change their polarisation or bearing angle in different levels of noise, but did swim closer together in more noisy conditions. I found no evidence that fish in pairs detected more prey than would be expected given the detection rates of individuals on their own, suggesting that fish in pairs are not benefiting from more efficient distribution of vigilance in more noisy conditions. There was some evidence, however, that fish relied more strongly on social information in noisy conditions, with fish becoming more correlated in their speed changes in increased levels of noise. My results suggests that at least in pairs of fish, the benefits of socially derived information in noisy conditions are limited.

4.1 Introduction

Animals can gather information from their environment either privately or by using social cues from other group members. Private information involves an individual gathering information directly from their environment (Dall et al., 2005). However, animals are limited in the amount and type of information that can be obtained in a given time, and environmental noise can add further uncertainty to information sources (see Chapter 2). Therefore noise can reduce the ability of individuals to gather information directly from their environment. One solution in group living species could be to take advantage of the information gathered by other individuals. By pooling imperfect estimates of the world around them, individuals in groups can make more accurate decisions than they could if alone (Krause et al., 2002; Ward and Webster, 2016). Larger groups of golden shiners (*Notemigonus crysoleucas*) are better able to track preferred darker regions of their environment even when visual noise is added to these areas (Berdahl et al., 2013). These fish use a decision rule that means they slow down when in darker, more favourable regions. By coupling this with social interactions, groups of fish are able to navigate an environmental gradient to reach a preferred local minimum meaning groups can outperform individuals in these noisy conditions.

Whether an individual uses social information can vary depending on the context. Individuals are more likely to use social information when they are more uncertain about their environment (Boyd and Richerson, 1988; Jones et al., 2019; Laland, 2004; Morgan et al., 2015). This could either be because they do not have information or because they have less experience in performing a task (Kendal et al., 2004). Therefore, individuals may be more likely to use social information when their perceptual abilities become compromised. *Lasius niger* and *Formica pratensis* ants, for example, rely less on private information and more on pheromone trails, a source of social information, when their perception is reduced under low light conditions (Beugnon and Fourcassie, 1988; Fourcassie and Beugnon, 1988; Grüter et al., 2011). They do this by increasing pheromone deposition in low light environments, and are more likely to follow pheromone trails rather than rely on memories to navigate (Jones et al., 2019). Therefore, some animals appear to change their reliance on social information when they are uncertain about their environment.

Moving animal groups, such as schools of fish, can also benefit from accessing information gathered by their neighbours. In these collectively moving groups, individuals use simple rules to respond to the position and movement of their neighbours (Rosenthal et al., 2015). First, these rules give the group its structure, and determine where individuals are located relative to one another, and therefore where individuals can sample information in the environment. For example, changes to the attraction or alignment rules of individuals give groups different cohesion and directional coordination, changing the area and angles over which information is detected by individuals in the group. Indeed, individual sticklebacks that are the first to respond to a food source do so more quickly when the shoal is in a more disordered state, which is likely due to the increased visual field of the disordered group (MacGregor et al., 2020). Second, responding to neighbours' movements or positions can also allow individuals to indirectly gain access to information about the direction or location of an otherwise undetected predator or food item (Ioannou et al., 2011, 2015; Lemasson et al., 2018). By copying the speed or directional changes of neighbours, individuals can indirectly copy movements away or towards predators or prey, respectively.

Much like how other social animals adapt their reliance on social information under times of uncertainty, moving animal groups may also change how they respond to their neighbours' movements and positions when their private information is compromised. In moving animal groups, this could have two consequences. First, changing social interaction rules could allow groups to distribute which regions of the environment individuals are scanning, changing individuals' positions and bearings relative to one another (e.g. their polarisation, bearing angle and separation distances (MacGregor et al., 2020; Rosenthal et al., 2015)). For example, acoustic noise reduces the spatial and directional organisation of juvenile seabass shoals (*Dicentrarchus labrax*), causing them to become less cohesive and less directionally ordered (Herbert-Read et al., 2017). Becoming less cohesive and polarised could be an adaptive mechanism by the fish to increase the overall area searched by the group, as the combined visual fields of all individuals would therefore cover more of the environment. Second, by changing how responsive individuals are to changes in their neighbours movements, this could in turn increase or decrease their likelihood of sampling social information. They could achieve this by copying the speed or directional changes of neighbours more accurately, becoming more correlated in their movements, or by reducing the delay in adopting changes to their neighbours' movements. Adapting interaction rules in times of uncertainty, therefore, may allow animal groups to improve information gathering and sharing in noisy environments. On the other hand, changes to group structure in noisy conditions may not be an adaptive response by individuals to mitigate the impacts of compromised perception. Instead, environmental noise could hinder an individual's ability to detect social cues, impairing the ability of individuals to coordinate their movements with neighbours. Whether changes to group structure in the presence of noise represent a constraint on social coordination, or an adaptation to increase information gathering in a social context, remains to be tested.

Here I investigated how a form of dynamic visual noise in aquatic environments, termed caustics, affects the degree of spatial and directional organisation and coordination of pairs of sticklebacks. Furthermore, I asked whether such changes in group structure and coordination may represent an adaptive strategy to increase the ability of pairs of fish to detect information in visually noisy environments. I predicted that if fish are more likely to distribute their search between group members in noisy conditions, they should be less cohesive and more disordered in their direction/orientation in higher levels of noise. Furthermore, if individuals are more responsive to social information in noisier environments, there would be an increase in the coordination between neighbours' speed and direction changes, with a decrease in the time delay between when individuals' movements were most correlated. Finally, I asked whether any changes in social behaviour may represent an adaptive strategy to increase the ability of fish to gather information when grouping in noisy environments. I predicted that being in a pair would make detecting virtual prey more likely than would be expected by simply having an additional pair of eyes. Moreover, I predicted that in higher levels of noise, being in a pair would mitigate a reduction in prey detection. In particular, the negative impact of noise on prey detection would be lower in pairs than for individuals on their own. To test this, I compared the prey detection rates of pairs of fish to a null baseline derived from the detection rates of individuals in different levels of noise.

4.2 Methods

4.2.1 Playbacks

Video playbacks of simulated caustics were projected into the same experimental arena as described in Chapters 2 and 3. I created caustic patterns to represent six different magnitudes of visual noise, by altering the speed at which these caustic patterns flickered. Each playback was composed of two temporal halves - the first half of each playback contained all six noise levels sequentially without the presence of virtual prey, while the second half of each playback contained all the noise levels with the addition of projected virtual prey. Each noise level occurred at different times (order-within-trial) in each half of the playbacks in a latin square design (Table 4.1). The noise levels and virtual prey were made using the same methods as in Chapter 2 and Chapter 3.

Table 4.1: Order that the different levels of noise were presented within each playback for the virtual prey experiments. The letter above each of the columns is the name of the playback. One playback (containing two halves) was given to each fish. For each half of the playbacks each noise level occurred at all different times in the six playbacks, in a latin square design.

Order within trial	**a**	**b**	**c**	**d**	**e**	**f**
First half of trial, prey absent						
1	2	3	1	6	4	5
2	4	1	5	2	6	3
3	1	5	4	3	2	6
4	6	4	3	1	5	2
5	3	6	2	5	1	4
6	5	2	6	4	3	1
Second half of trial, prey present						
7	1	5	2	3	6	4
8	5	3	4	1	2	6
9	4	6	1	5	3	2
10	3	2	6	4	1	5
11	2	4	3	6	5	1
12	6	1	5	2	4	3

4.2.2 Study subjects

Three-spined sticklebacks were caught from the river Cary in Somerton, Somerset, UK (51.069990 latitude,-2.758014 longitude) in March 2019. All fish were housed and fed using the same methods as described in Chapters 2 and 3. Fish were left to acclimate to captivity for at least two months before experimentation. Fish were not fed for 24 hours prior to experiments and fish that would be used in the subsequent day were placed in the holding area of the arena overnight, allowing them to acclimate to the conditions of the tank.

4.2.3 Experimental protocol

For each day of trials, four experimental trials were run, two with individual fish and two with pairs of fish. The number of fish used in a trial alternated within a day and the number of fish used for the first trial of the day alternated between days. The sex of the fish was not recorded. Each trial began with the fish experiencing six levels of noise with no prey projected, so that I could test how fish adapted their movements and social behaviour in the absence of virtual prey. The second half of the trial involved six levels of noise with prey projected over the caustics so the ability of pairs and individuals to respond to the prey could be compared. At the start of the experiment, the fish were given 10 minutes of acclimation time where the lowest level of noise was projected onto the bottom of the test arena (as in Chapter 2). Experimented fish were removed and placed in a separate housing tank to ensure that they were not reused in later trials and were then fed. Fish tested as individuals were not used in trials as pairs, and fish tested as pairs were not retested as individuals.

4.2.4 Tracking and analysis

Fish were tracked using the software Loopy (loopbio gmbh, 2015) which implements image recognition and tracking using a supervised learning method termed ‘key point detection’. By annotating reference images, I trained the algorithm to detect the head and tail of the fish, which could then be tracked during each trial. Tracks (x and y coordinates of each fish) were then imported into MATLAB. I assessed the tracking accuracy for trials that contained two fish by calculating the proportion of frames where both the head and tail of both fish were present. Both the mean and median tracking accuracy across all these trials was >90%. A selection of tracks for each trial were also visually inspected.

For the pairs of fish, measures associated with the cohesion and coordination of the fish’s movements were calculated from the tracks from the first half of the trial (Figure 4.1a). Each metric was calculated for each noise level in each trial. First, I explored how fish change their spatial and directional coordination as this would give insight into how fish are searching different areas of their environment. The modal distance between the two fish was measured, taken from the kernel density histogram of distances across all frames within a noise level. The median absolute bearing angle of each fish relative to the other was also calculated. This is a measure of the positioning of a fish with regards to a focal individual, and gives information on where in the visual field a neighbour is located. The bearing angle could vary between 0 degrees (directly in front) and 180 degrees (directly behind), with a bearing of 90 degrees representing a neighbour that is directly to the side of the focal fish. I separated instances when the neighbour was behind (> 90 degrees) or in front of the focal fish (< 90 degrees) and took the median angle at which the neighbour was located for these two categories separately to test if the bearing angle changed in response to noise. Finally, I tested the polarisation of the fish, which is a measure of the alignment of the fish in the group relative to one another. To do this, for each frame I first calculated the unit vectors of the two fish from the head and tail coordinates, summed these unit vectors, and divided the length of the resultant vector by two. Polarisation scores ranged from 0 (individuals facing in different directions) to 1 (individuals facing in the same direction) (Couzin et al., 2003). The proportion of time that the fish had a polarisation score of >= 0.85 was then calculated for each noise level in each trial as a measure of when the fish were in a highly coordinated schooling state (Jolles et al., 2017; MacGregor et al., 2020). The mean mean speed of both fish was also measured across each trial by taking the mean speed of the two fish in each frame and then finding the overall mean for the trial.

To test whether noise induced fish to become more correlated in their speed or directional changes, I calculated the cross correlations in direction (Figure 4.1b) and speed between the two fish so that the time lag and magnitude of the maximum correlation (as in Nagy et al. (2010)) could be explored as a function of noise. Only segments without any missing tracks were used. To calculate cross correlations, I first split the trajectories into four-second chunks (equating to a cross correlation of two seconds before and after the movement of the focal fish). This window length was chosen by watching the fish and visually determining an appropriate delay in movement between the pairs (confirmed by assessing the decay in the cross-correlations after two seconds in subsequent analyses). To calculate the two measures of direction correlation, the vector of direction of the focal fish at all time points in the four second window was multiplied with the direction vector of the other fish at time point 0 in that window by taking the dot product. The time point in the resulting vector with the greatest value then gave the magnitude of the maximum direction correlation and the index or position of the time point within the window gave the value of the time lag. To calculate the cross correlation in speed, the function *xcorr* was used in MATLAB 2019a. This function returns the cross-correlation value of two signals (a and b). In other words it is a measure of the similarity between signal a and shifted (time lagged) copies of signal b. In my case the inputs to the function were the two vectors of speeds of both fish across each four second window. The magnitude and time lag of the maximum correlation in speed were then taken from the greatest value and its position in time, as for the direction correlation. The values for the time delay of maximum correlation and absolute correlation were calculated as a median throughout each noise level for each trial. Because the fish were generally highly polarised within some point in time (median absolute cross correlation across all trials = 0.99), only the time lag of the maximum value in direction correlation was measured. For the cross correlations in speed, the time lag of the maximum cross correlation was typically zero. Therefore, only the maximum absolute value of the cross correlation in speed was taken as a measure of speed coordination.

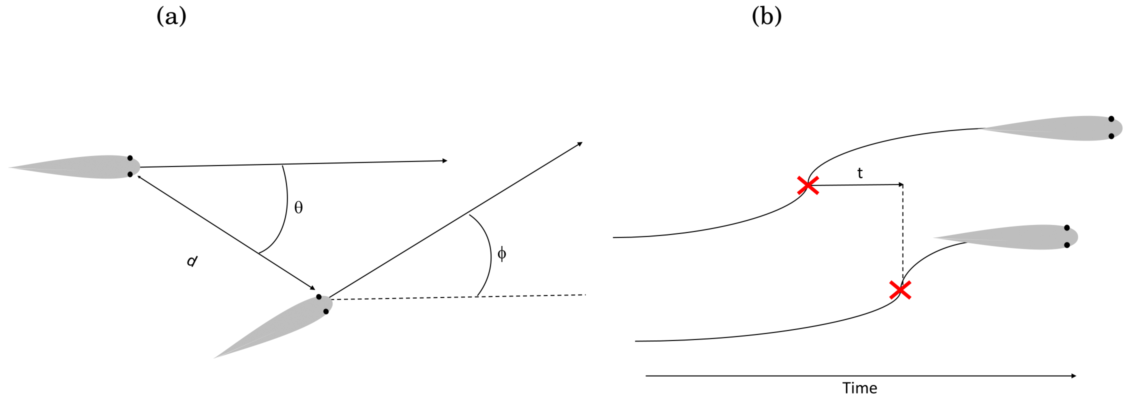


Figure 4.1: Calculating the different measures of cohesion and coordination between pairs of fish. a) The distance (d), the bearing angle (θ) and the polarisation (ϕ) can be quantified from the tracks of the two fish. b) The time lag (t) at maximum direction correlation can be quantified from the tracks.

To test whether any changes in the group structure or coordination of the fish have any influence on their prey detection abilities in different levels of noise, the prey sections of the trials were manually inspected to determine whether the fish responded to the prey. As in Chapter 2, a response to the prey was defined as when there was a noticeable change in the speed or direction of the fish towards the prey (Ioannou and Bartumeus et al. 2011) and I quantified how many prey the fish responded to in each noise level. For the pairs of fish, if either of the fish responded to the virtual prey, then the timing of the first response was recorded. To understand if the detection rates of pairs was higher or lower than would be expected given double the pairs of eyes, I calculated the null expectation of two pairs of eyes independently detecting information given the detection rates of individuals on their own. A null distribution of the detection rates of pairs in each level of noise was created by randomly taking bootstrapped samples from the known detection rates of two separate individuals, repeated 999 times. These randomly sampled detection probabilities of individual fish were then put into the below equation to calculate the probability of two independent individuals (A or B) detecting the prey, where P(A) and P(B) are probabilities that individual A or B detected the prey, respectively :

$$\text{Probability of detection} = P(A) + P(B) - P(A) * P(B)$$

The distribution of observed probabilities of pairs responding to the prey in different noise levels were then compared to this null distribution using Kolmogorov-Smirnov (K-S) tests. These distributions were compared for each noise level separately.

4.2.5 Statistics

All statistics were performed in R 3.5.1 (R Core Team, Version 3.5.1). Model comparison was done using the *Anova* function in the car package in R (Fox and Weisberg, 2019). A Type 2 Anova was run with the Chi-squared test statistic to test for significance of the fixed effects. Any non-significant effects were removed from the model before final analysis.

To explore whether the modal distance between the two fish changed as a function of noise, I fitted a linear model using the lme4 package (Bates et al., 2015), with noise as the fixed effect and trial as a random intercept. A square root transformation was applied to the modal distance between the pairs of fish, as there was some positive skew in the data. For the bearing angle, two linear mixed models (Bates et al., 2015) were constructed with noise level as the fixed effect and trial as a random intercept. Models were run separately for angles below and above 90 degrees for when the second fish was in front or behind the focal fish respectively. To explore whether the polarisation of the two fish changed as a function of noise, a generalised linear mixed model (GLMM) with beta error structure was constructed using the package glmmTMB (Brooks et al., 2017). Noise level, median speed and the median distance between fish were added as fixed effects and trial was added as a random intercept. For the bearing angle, two linear mixed models (Bates et al., 2015) were constructed with noise level as the fixed effect and trial as a random intercept. Models were run separately for angles below and above 90 degrees. For the mean speed of the fish, a linear model in the lme4 package (Bates et al., 2015) was constructed with noise as the fixed effect and trial as a random intercept.

When exploring how the time lag of the maximum correlation in direction varied with noise, a linear model was constructed using the lme4 package (Bates et al., 2015), with square root transformed median time lag included as the response variable, noise level included as a fixed effect and trial as a random intercept. For the magnitude of the cross correlation in speed, I constructed a linear model (Bates et al., 2015) with noise level, order in trial and polarisation as fixed effects, and trial included as a random intercept. Polarisation was included as a fixed effect because correlation in speed is highly likely to be influenced by the degree of polarisation between individuals if this is making it easier for individuals to detect movement cues. Due to the heavy tails of both these response variables, I used the LambertW (Goerg, 2015, 2020) package in R to transform the response variable to a gaussian distribution. To do this, I first used the *MLE_Lambert* function to estimate the parameters of the distribution and then back-transformed the data using the *get_input* function.

To test how the number of responses to the prey was affected by the number of fish and the noise level, a generalised linear mixed model with a negative binomial error structure was constructed using in the lme4 package (Bates et al., 2015). The noise level and number of fish were added as fixed effects and trial was added as a random intercept. To compare the detection probabilities for the pairs of fish to the null expectations (calculated in section 4.2.4), Kolmogorov-Smirnov tests were used.

4.3 Results

I first explored the changes in spatial coordination between the pairs of fish in response to noise. Pairs of fish swam closer together in higher levels of noise (Figure 4.2a; LMM; $\chi^2 = 17.9, df = 1, p < 0.001$). While fish generally appeared to be more likely to be behind or in front of the focal individual rather than to the side (Figure 4.2b), the bearing angle of the fish when the neighbour was either in front or behind the focal individual was not significantly affected by noise (neighbour in front: Figure 4.2c; LMM; $\chi^2 = 2.39, df = 1, p = 0.12$; neighbour behind: Figure 4.2d; LMM; $\chi^2 = 1.80, df = 1, p = 0.18$).

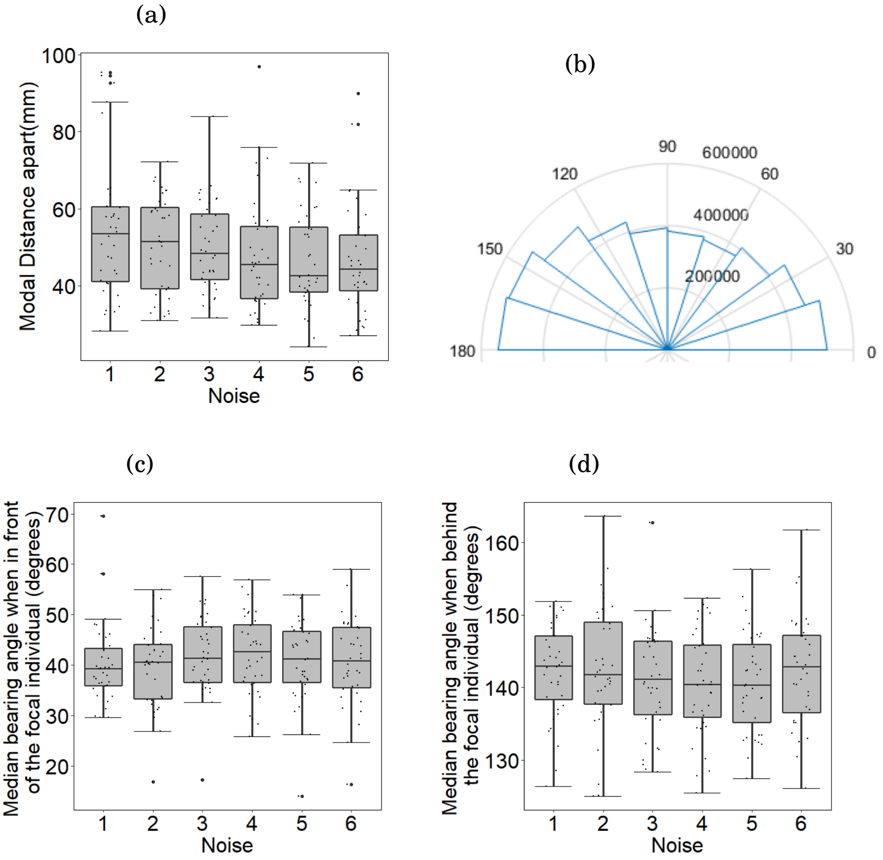
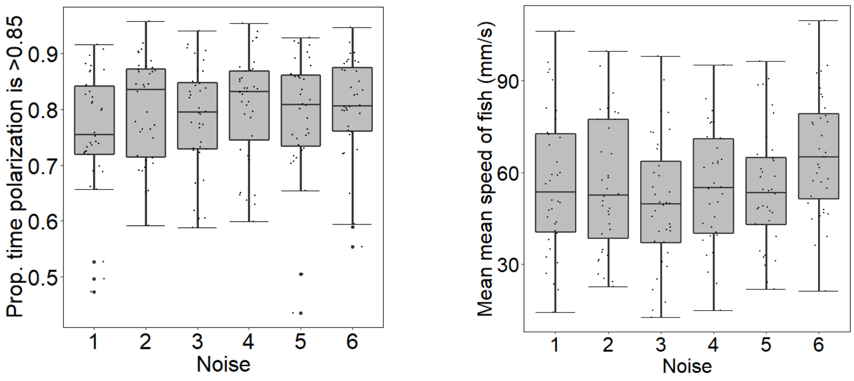


Figure 4.2: Spatial positioning of the fish as a function of noise level. a) The modal distance between the fish taken from the kernel density decreases as a function of noise. b) All bearing angles of the neighbour fish in relation to the focal fish. Fish appear more often behind or in front of the focal individual. The numbers around the outer edge give the angular position of the neighbour relative to the focal fish in degrees, while the rings inside the plot denote the frequency. Angles of 0 degrees indicate the fish was directly in front of the focal fish whereas angles of 180 degrees indicate the fish was directly behind. c) Bearing angle when in front of the focal individual did not change as a function of noise d) and the bearing angle when behind the focal individual does not change as a function of noise. The central line of each box shows the median value while the upper and lower lines of the box show the upper and lower quartiles of the data. The whiskers extend to the most extreme data point within 1.5 × the interquartile range. Jittered points represent raw data points.

I next tested whether noise had any influence on the directional organisation of pairs of fish. While the proportion of time the two fish were highly polarised (> 0.85) appeared to increase with noise level (Figure 4.3a), this effect could be explained by pairs of fish swimming faster in higher levels of noise (4.3b; LMM; $\chi^2 = 6.5, df = 1, p = 0.01$). Therefore, polarisation was not influenced by different levels of noise (Figure 4.3a; GLMM; $\chi^2 = 0.48, df = 1, p = 0.49$), but did increase with the median speed of the two fish (GLMM; $\chi^2 = 21.7, df = 1, p < 0.001$) and decreased the further the fish were apart (GLMM; $\chi^2 = 52.8, df = 1, p < 0.001$).



(a)

(b)

Figure 4.3: How noise affects the movement dynamics of the two fish. a) Polarisation of the fish does not change in different levels of noise. b) The mean mean speed of the fish increases as a function of noise. The central line of each box shows the median value while the upper and lower lines of the box show the upper and lower quartiles of the data. The whiskers extend to the most extreme data point within 1.5 × the interquartile range. Jittered points represent raw data points.

Next, I explored the direction and speed correlations of the fish and asked if they were impacted by noise. The time lag between the two fish's maximum correlation in direction increased with noise (Figure 4.4a; LMM; $\chi^2 = 5.94, df = 1, p = 0.015$) and the magnitude of the cross correlation in speed increased with noise (Figure 4.4b; LMM; $\chi^2 = 20.4, df = 1, p < 0.001$). The magnitude of the cross correlation in speed also increased later on in the trial (LMM; $\chi^2 = 5.82, df = 1, p = 0.016$) and when the fish were more polarised (LMM; $\chi^2 = 6.23, df = 1, p = 0.013$).

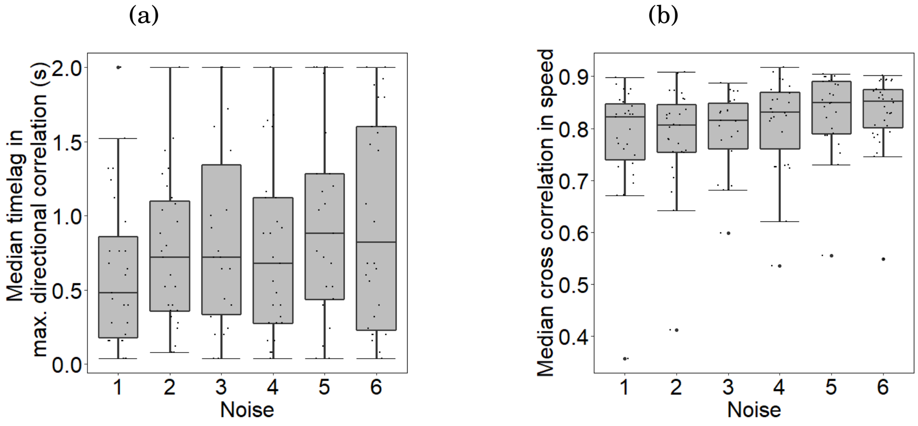


Figure 4.4: Correlations in direction and speed between the two fish. a) The median time lag in the maximum direction correlation of the two fish increased with noise. b) The median magnitude of the maximum cross-correlation in speed of the two fish increased with noise. The central line of each box shows the median value while the upper and lower lines of the box show the upper and lower quartiles of the data. The whiskers extend to the most extreme data point within 1.5 × the interquartile range. Jittered points represent raw data points.

The number of responses to prey decreased in higher levels of noise (Figure 4.5; GLMM; $\chi^2 = 21.6, df = 1, p < 0.001$) and increased with the number of fish (Figure 4.5; GLMM; $\chi^2 = 16.9, df = 1, p < 0.001$). There was no interaction between number of fish and noise level on the number of responses to the prey (Figure 4.5; GLMM; $\chi^2 = 0.18, df = 1.p = 0.67$). When comparing the observed values of the fish to the null expectation (the number of prey expected to be detected if there were two fish exploring independently), there was no difference between the distributions for any noise levels (Figure 4.6); K-S test; Noise 1; D=0.12, p=0.73; Noise 2; D=0.062, p =0.99; Noise 3; D=0.11, p = 0.80; Noise 4; D = 0.13, p = 0.61; Noise 5; D = 0.12, p = 0.65; Noise 6; D=0.13, p = 0.57).

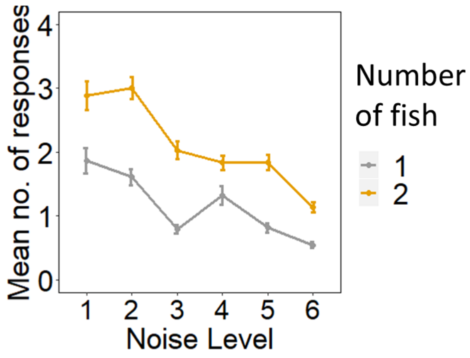


Figure 4.5: Mean number of responses to the prey in different levels of noise when there were both one (grey line) and two (yellow line) fish present. Pairs of fish consistently detected more prey than individuals, and as the noise level increases, the number of detections decreases. Error bars show the standard error.

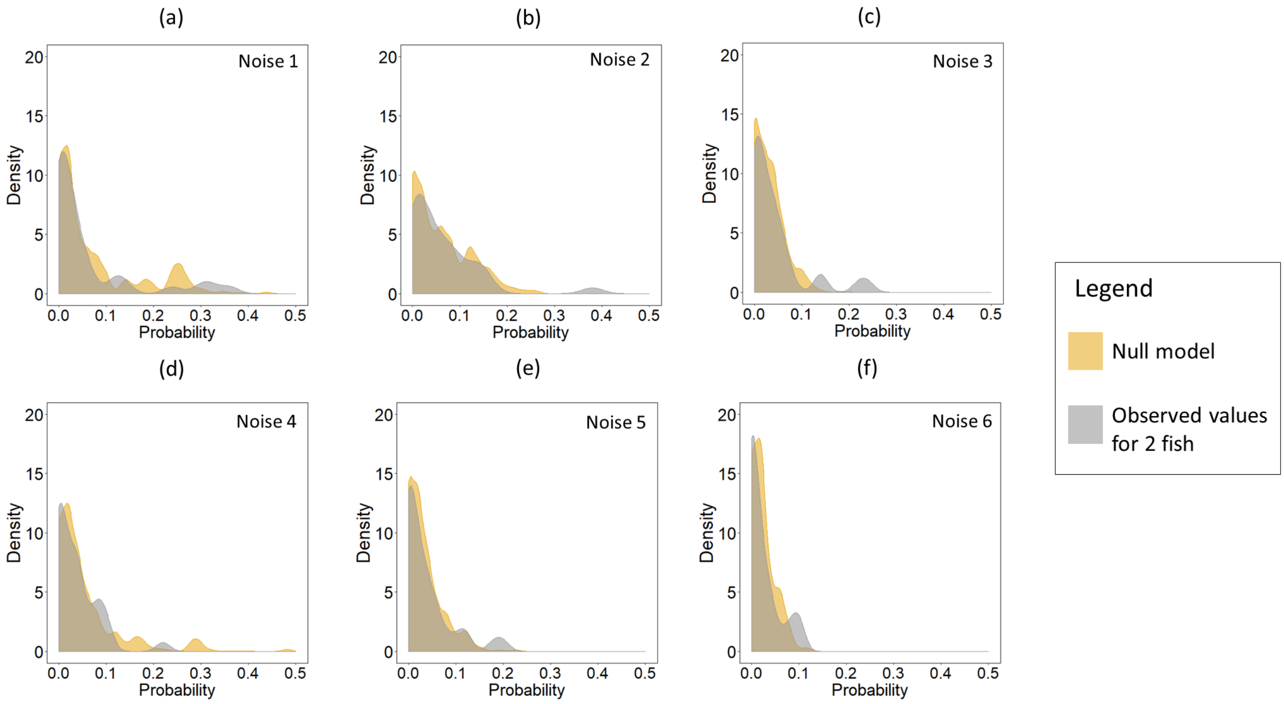


Figure 4.6: The probability that at least one fish detected the prey for each level of noise. Probability density distributions in grey represent the observed probabilities of two fish responding to the prey, whereas distributions in yellow were calculated from the detection probabilities of individuals assuming that individuals detect information independently (null model). a) Probability density function for Noise 1 b) Noise 2 c) Noise 3 d) Noise 4 e) Noise 5 and f) Noise 6. There was no statistical difference between any of the null and observed distributions.

4.4 Discussion

In this chapter, I tested whether the spatial structure and coordination of fish changed in different levels of noise and asked whether these changes acted to increase detection rates of pairs of fish in noisier conditions. While there was no evidence of noise-induced changes in the bearing angles or polarisation of the two fish, I found evidence that fish swam closer together in high levels of visual noise. These changes to group structure, however, did not appear to improve the detection abilities of pairs in noisy conditions. I also found that pairs were more correlated in their speeds in higher levels of noise, suggestive of increased information sharing in noisy conditions.

Pairs of fish swam closer together in noisier conditions. Indeed, this finding is consistent with other recent work showing that sticklebacks show greater attraction towards shoals of conspecifics in higher levels of visual noise (Matchette and Herbert-Read, 2021). There was no evidence, however, that visual noise affected the directional organisation of the pair or the bearing angle to their neighbours. There does not appear to be evidence, therefore, that individuals are more likely to distribute their visual search in higher levels of noise to compensate for individually reduced perception. Instead, by moving closer together, the fish would instead have had more overlapping regions of their visual fields. While not increasing the total area that was scanned, this could instead increase the likelihood that the pair detect information, such as the presence of predators or prey, in the areas they are moving through. In effect, this could increase the reliability that the pair detected information in the limited areas they were scanning. Alternatively, increased cohesiveness in higher levels of visual noise could be a result of individuals attempting to reduce their risk in noisier environments. By moving closer together, individuals can reduce their domains of danger (Hamilton, 1971), and this may be particularly important in conditions where predators may be more difficult to detect, such as in higher levels of visual noise. My results from Chapter 3, however, suggest individual fish did not adjust their risk-taking behaviour in terms of refuge use in more visually noisy conditions, so this explanation may be less likely. Therefore, stronger cohesion could be a mechanism to increase overlap of visual fields in noisier conditions.

Moving closer together in increased levels of visual noise could also be a response to make it easier for fish to pick up on movement cues from one another. Indeed, the use of visual cues to maintain cohesion is common in many animals that move in groups (Grünbaum, 1998; Herbert-

Read, 2016; Herbert-Read et al., 2017; Partridge and Pitcher, 1980; Pitcher, 1979), and therefore swimming closer together in increased noise could allow individuals to detect the movements and positions of neighbours more effectively. However, there was conflicting evidence of whether the social coordination of individuals was affected by visual noise in this study. Indeed, while the time lag between the maximum directional correlation of the fish increased in higher levels of noise, suggestive of reduced directional coordination between the pair, the two fish became more correlated in their speeds in higher levels of visual noise. Speed changes appear more important than direction changes in coordinating movements of many species of fishes (Herbert-Read, 2016; Herbert-Read et al., 2017; Katz et al., 2011). If changes in speed provide individuals with information about the detection of predators or prey as they do in other species, increasing speed correlations, therefore, could improve individuals' access to social information in more visually noisy conditions (Herbert-Read et al., 2015). Having stronger coupling of speed changes could allow individuals to scrounge from the limited amounts of information that are detected in noisy conditions, allowing individuals to acquire resources or avoid threats more effectively in noisy conditions. However, having stronger coupled movements may not always be beneficial. Cascades of false information (Laland and Williams, 1998) and competition for shared resources (Lima, 2021) can make copying others costly. In larger groups, such social information use may be particularly costly, as false positives scale with increasing numbers of individuals. Assessing how individuals' coordination in larger groups is affected by noise, in particular asking whether there are reductions in coordination in higher levels of visual noise, would be a future direction for this work.

When investigating the correlations in movement of the pairs of fish I found that the two fish became more correlated in their speed. This could be a strategy to increase efficiency in the transfer of social information between individuals in more visually noisy conditions. The speed cross correlation between pairs also increased when the fish were more polarised, suggesting that increased polarisation makes it easier to match speeds. This would make sense if the increased polarisation is allowing the fish to more easily use cues from the movement and position of their neighbours to coordinate movement (Ioannou et al., 2011; Lemasson et al., 2018). Conversely, the time lag of the maximum direction correlation between the fish increased in higher levels of noise. The fish were often highly polarised (directionally correlated) regardless of the level of noise, but this increase in delay time between fish being most directionally correlated could be because noise was impairing the fish's ability to pick up on a neighbour's movement cues. However this then contradicts with the increase in speed correlation. Perhaps dynamic visual noise has a greater impact on a fish's ability to detect cues used to align with neighbours compared with cues used to match speeds. Alternatively this increase in time lag could be an adaptive strategy by pairs of fish to increase the search area covered by the pair. If facing in different directions at a given time, this increases the likelihood that at least one individual in the pair or group will detect the prey, or an attacking predator (MacGregor et al., 2020).

To test whether the observed changes to group structure may have had some functional role in increasing the likelihood of pairs detecting prey, I compared the detection rates of prey for individuals and pairs of fish. The likelihood of responding to the virtual prey decreased in higher levels of noise both when fish were in pairs or alone. These results are consistent with those of Chapter 2, suggesting that noise places a perceptual constraint on the fish's ability to detect prey. While pairs of fish detected more prey overall than individuals, this is expected due to the additional eyes of two versus one individual. If the pairs were benefiting from dividing information gathering more efficiently in noisy conditions, however, we would have expected an interaction between noise and the number of fish on the detection rate of the prey. The absence of this interaction suggests these changes in the group structure do not appear to counteract the effect of noise on individual visual perceptual abilities. Indeed, when comparing the observed proportion of detections for pairs of fish with the null expectation that the two fish were exploring independently, there was no difference between the null and observed detection rates. Indeed, other animals also fail to efficiently distribute vigilance patterns amongst themselves. Ostriches (*Struthio camelus*) for example, do not adjust the timing of their vigilance bouts with other group members to scan for predators more efficiently (Bertram, 1980). It is worth noting, however, that in my study, the visual ranges of the two fish are unlikely to be independent, as the fish are coordinated in their movements and therefore exploring similar space. We might predict, therefore, that the expected detection rates of the two fish should be even lower than this independent search model. Future work could account for this by deriving a more spatially explicit model of the expectation that the fish would detect information in their visual fields. This model could be informed from the data in Chapter 2, where distance, angle and speed of a fish determines if and where detections occur in the visual field. While beyond the scope of this PhD, this model would allow me to infer whether there could be any added benefit of collectively searching for prey together.

In conclusion, I find that visual noise reduces the ability of individuals and pairs of fish to detect information in their environment. While pairs of fish swam closer together in noisier environments, other aspects of their spatial and directional configurations did not change. In noisier environments, fish became more correlated in their speed, but had longer time delays between their maximum directional correlations. I find no evidence to suggest that these changes in coordination increased the ability of pairs to detect information compared to individuals. These results suggest that changes in group structure in response to noise do not appear to increase the ability of pairs to detect information, but that individuals may improve their speed coordination to make use of any social information that is detected.

CHAPTER 5

SOCIAL VERSUS PRIVATE INFORMATION USE IN WEAVER ANTS

Due to Covid related travel restrictions the lab experiments for this chapter were carried out by Justin McNab, Madelyne Stewardson and Lisa Safranek at Macquarie University. I was still responsible for the experimental design, video and data analysis, and writing.

Animals' perceptual capabilities can be compromised by environmental noise, reducing their likelihood of detecting important cues or signals in their environment. How might animals alter their behaviour in response to these constraints placed upon their perception? One way could be to increase reliance on social information. Indeed, many ant species use pheromones as an important source of social information, and sometimes rely on pheromone trails instead of using their own personal information, such as route learning, to navigate. Here, I tested whether weaver ants (*Oecophylla smaragdina*) rely more or less on social information in visually demanding environments. To do this, I immersed ants into environments with differing levels of visual noise (simulated dappled light), and measured their activity and pheromone laying behaviour in these visually noisy environments. The weaver ants experienced high and low levels of visual noise, with dappled light moving at different speeds, along with controls of a static noise background and uniform light. The activity levels of these ants generally did not vary with noise level, and there was no difference in recruitment to food sources in different levels of noise. In the static and uniform treatments, the number of ants laying pheromone declined more rapidly over the course of the experiment, whereas in the higher noise treatments, ants laid pheromones at a consistently higher rate. Therefore, ants lay more pheromone in higher noise levels but did they choose to rely on pheromone more? When given a choice between a longer route containing social information (pheromone trail) and a shorter, more efficient, route lacking these cues in different levels of noise, ants were quicker to choose the shorter route in lower levels of noise and took longer to find this route in higher levels of noise, preferring instead to initially follow the pheromone trail. My results highlight that these ants could be mitigating the effects that environmental noise has on their perceptual abilities by increasing their reliance on social information in times of increased noise and this may compensate for any negative impacts imposed on them by noise.

5.1 Introduction

Animals can gather information from multiple sources, and choose which of these to rely on, particularly when they conflict. In groups of unrelated individuals, animals can use social information to inform their decision making but this social information is often simply cues about the location or movements of neighbours. Indeed, in unrelated groups, sharing of information is often simply a by-product of individuals responses to food or predators (Danchin et al., 2004) and such costly behaviour has the potential to be exploited by other individuals. In Chapter 4, I found that individuals may rely more on social information in times of compromised perception but that the benefits of social information are limited, at least for pairs of fish foraging in noisy conditions. However, groups of highly related individuals have increased benefits of sharing information and therefore may be more likely to have behavioural mechanisms to mitigate the impacts of noise by actively sharing and signalling social information. Groups of insects exist on a wide spectrum of sociality from solitary individuals to eusocial groups (Leonhardt et al., 2016). Ants, termites and some bees and wasps are eusocial which means that individuals form persistent groups and divide labour. This includes many individual workers giving up their own reproduction in order to help others in the colony reproduce. This, however, still produces fitness benefits for these sterile workers due to the high genetic relatedness of individuals in the colony (Hamilton, 1972; Queller and Strassmann, 1998). This high relatedness between individuals means that cooperation between group members is more likely to evolve (Bourke and Franks, 2019; Hamilton, 1963), leading to behaviour that is more collective than witnessed in fish shoals or bird flocks.

These cooperative mechanisms have lead to an interesting array of communication forms evolving in the social insects. For example the waggle dance in bees (Frisch, 1967), stridulation in crickets (Pollack, 1990), tactile communication (attennation) in termites (Reinhard and Clément, 2002) and hymenoptera (Hölldobler and Wilson, 1978) and finally pheromones, information-carrying chemical compounds produced by many insects for intraspecific communication (Leal, 2005; Wyatt, 2014). Indeed, many ant species use signals to coordinate their behaviour between group members. In particular, ants can indirectly coordinate each other's activity by depositing and responding to pheromone trails (Hölldobler et al., 1990; Reid et al., 2011; Theraulaz and Bonabeau, 1999). These pheromones are a source of social information that individuals can use to locate a food source, locate a territory or warn others of danger. This allows collective sensing of the environment within colonies meaning individuals can benefit from information gathered by other individuals (Theraulaz and Bonabeau, 1999).

In environmental conditions that challenge individuals' perception, such as in low-light or fluctuating light levels, it may be adaptive for the individual to rely more on social information encoded in pheromone trails than on their own route memory guided by visual perception. Indeed, in low-light conditions, *Lasius niger* ants increase deposition of pheromone and choose to rely less on their own private information and instead rely more on pheromone trails when navigating (Jones et al., 2019). Therefore, individuals can switch which information source they rely on when uncertain, and aid the navigation of others when navigation becomes more difficult. *Lasius niger* ants can also increase their pheromone deposition after experiencing a change in the location of a food source in their environment, helping to maintain robustness while the colony is foraging. Those ants that make navigational errors while foraging lay less pheromone when searching for the food source but increase their pheromone deposition when returning to the nest (Czaczkes et al., 2013; Czaczkes and Heinze, 2015). This suggests that ants can regulate the amount of pheromone they lay depending on their navigational certainty and can also increase deposition in challenging navigational situations to aid other colony members.

Pheromone laying behaviour is a unique system that can be used to quantify social information use in social insects. Here, I explored whether pheromone laying behaviour and reliance on pheromones changed in different levels of visual noise in the weaver ant (*Oecophylla smaragdina*). Weaver ants live in very large colonies of up to 500,000 female workers that nest in the tree canopy but forage for a wide variety of food items both among the trees and on the ground (Hölldobler and Wilson, 1977). They rely on both visual cues and pheromone trails to navigate (Hölldobler and Wilson, 1977), making them an ideal system to investigate the use of both private and social information. To test this, I first explored whether the activity levels and movement characteristics of ants are affected by dynamic visual noise using simulated dappled light. This dynamic light pattern mimics the effect of light filtration through a leaf canopy, which is a highly relevant environmental stimulus for these arboreal insects. With these activity metrics I could explore if noise affected recruitment of ants to and from food sources as this would affect how much food enters the colony which, in turn, could have fitness consequences on the colony. I next asked whether the ants increased pheromone deposition, a source of social information, while foraging in different levels of dynamic visual noise. If the visual noise is acting as a perceptual constraint on individuals, potentially impacting the use of visual navigation cues, then I predicted their pheromone laying to increase in higher levels of noise to improve the collective decision making of the colony. Finally, to confirm whether ants relied more on social information in increased levels of visual noise, ants were given a choice to travel down a longer path that contained social information (a pheromone trail), or a shorter path that did not contain a pheromone trail but should be preferred due to its higher efficiency (Goss et al., 1989). If ants rely more on following social information in increased levels of visual noise, I predicted that ants would be more likely to choose the pheromone trail in noisy conditions, but would be more likely to choose the shorter, more efficient route in less noisy conditions.

5.2 Methods

5.2.1 Study subjects

Four colonies of *Oecophylla smaragdina* were kept in temperature-controlled rooms at Macquarie University, North Ryde campus (NSW, Australia) in 25-30^oC, with 80-100% humidity. Each colony contained a queen and brood as well as workers of minor and major caste, estimated to contain 2,000 - 5,000 workers. These colonies were fed on a diet of honey water (50% v/v) ad libitum with house crickets (*Acheta domesticus*). twice a week. Three Domus Class 2 18W LED lights were suspended above the colonies in a 12L/12D photoperiod which started at 6:00am each day. These colonies had been kept in the above conditions for a minimum of 19 months. Smaller sub-colonies of 200 major caste workers were made from each colony for every replicate in both experiments. These sub-colonies were only tested once and had no access to food for at least 12 hours before experiments commenced to encourage foraging behaviour. Experiments were performed in 25^oC with 30-50% humidity, in a separate temperature-controlled room.

5.2.2 Light conditions

A ChauvetDJ Abyss USB projector was used to create the visual noise. This used a singular LED with circular disks in front that could be set to oscillate at various speeds. As these disks move past and overlap with one another this creates dark and light regions similar to dappled light, creating varying levels of visual noise. The following four noise level treatments were used to test each of the sub-colonies: high noise, low noise, static noise and uniform light/no noise. To create the uniform light treatment a single 18W LED panel was used, with the projector turned off. For the static, low and high noise conditions “Stop”, “33 right rotation” and “100 right rotation” respective settings were used. With these settings, the static noise projected a stationary dappled light, the low noise was a slowly moving light field, and the high noise treatment moved three times faster than the low noise treatment. The intensities of each light condition were measured three times and then averaged using a Li-cor (Li250) light meter. The high, low and static visual noise treatments were made up of bright and dark patches that oscillated at different speeds. Bright patches had a mean light intensity of 40.5 µmol and dark patches had an average light intensity of 3.15 µmol. The uniform light treatment was measured as 21.4 µmol, which is approximately the average of the light and dark spots created in the other three noise treatments.

5.2.3 Experiment 1 - Pheromone laying

To test whether ants alter their pheromone laying behaviour in different levels of noise, a plastic platform with a thin bridge leading to a food source of honey water (50% v/v) was used as the testing arena (Figure 5.1). This arena had the noise projection centred on the bridge leading to the food. Each replicate was recorded with two Panasonic DMC-GH4 DSLR cameras with one filming laterally and one dorsally. The lateral camera was equipped with a Panasonic Lumix G 30mm macro lens while the dorsal camera was equipped with a Panasonic Lumix G 14-42mm lens. Each camera recorded in 4K resolution, at 24 frames per second. In this experiment, each colony experienced each level of noise three times giving a total of 48 trials (four colonies x four noise levels x three replicates). These experiments were carried out in a pseudo-randomised order with each noise treatment and colony used at different times on different days (Table 5.1). Experiments ran for 30 minutes from when the first worker returned from the food source back to the sub-colony container. Once a trial was completed, the workers were returned to their original colony. The likelihood of ants being re-used in sub-colonies was very low due to the large size of the original colonies (2,000 - 5,000 workers).

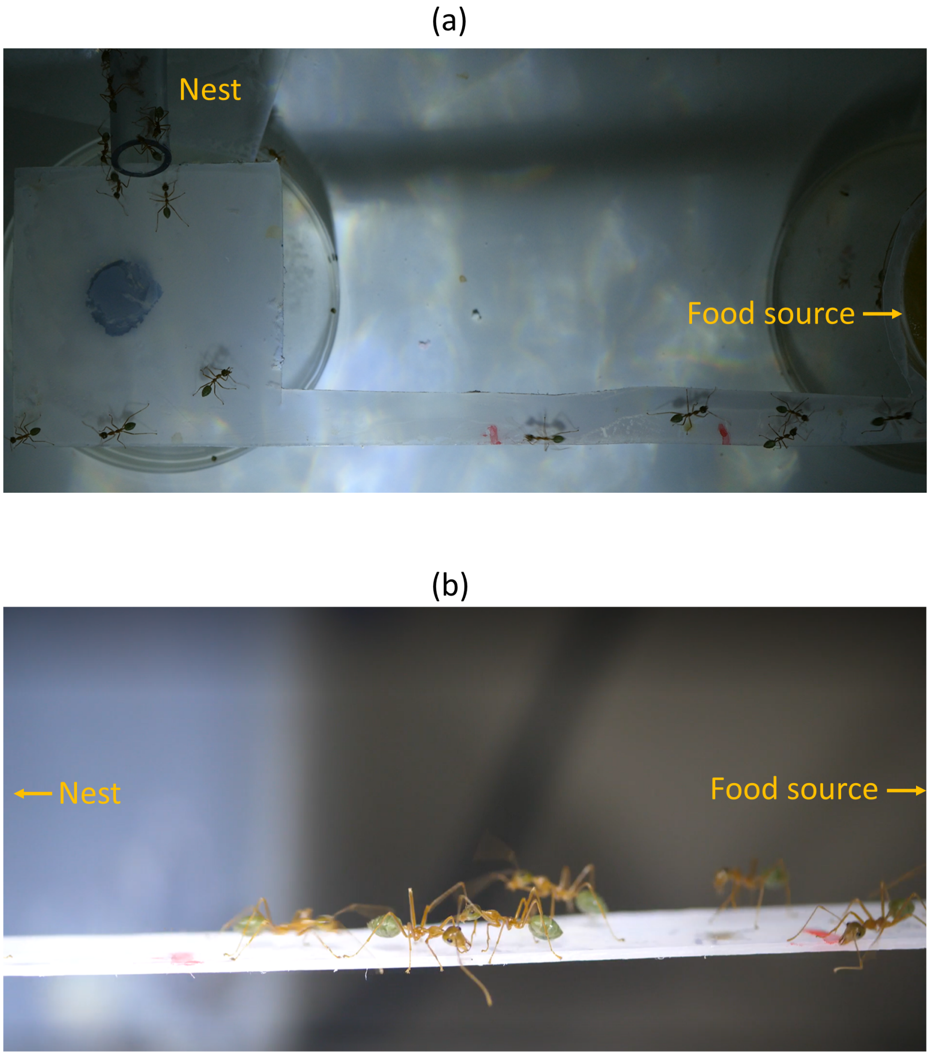


Figure 5.1: Set-up for the pheromone laying experiment with the two camera views a) The dorsal camera view which was used to extract the activity measures of the ants b) The lateral camera view of the experiment which was manually scored to quantify the pheromone laying dynamics of the ants.

Table 5.1: Order that the different treatments were presented to each colony. Each colony experienced each noise treatment three times, therefore giving a balanced design.

Trial number	Colony	Treatment
1	1	Static
2	2	High
3	3	Uniform
4	4	Low
5	3	Static
6	4	Uniform
7	1	High
8	2	Low
9	4	High
10	3	Low
11	2	Static
12	1	Uniform
13	3	High
14	4	Static
15	1	Low
16	2	Uniform
17	4	Static
18	1	High
19	2	Uniform
20	3	Low
21	1	Uniform
22	2	Static
23	4	Low
24	3	High
25	2	High
26	1	Low
27	3	Static
28	4	Uniform
29	2	Low
30	3	Uniform
31	4	High
32	1	Static
33	1	Low
34	4	Uniform
35	3	High
36	2	Static
37	2	Uniform
38	3	Low
39	1	Static
40	4	High
41	3	Uniform
42	4	Static
43	2	Low
44	1	High
45	4	Low
46	2	High
47	1	Uniform
48	3	Static

Movement metrics - To explore the activity parameters of the ants, the dorsal videos (Figure 5.1a) were tracked using the software Loopy (loopbio gmbh, 2015) as in Chapter 4. By annotating reference images, I trained the algorithm to detect the head and gaster of the ants. The algorithm was trained on a total of 2140 frames across 40 video segments (each trial was split up into video segments of ~ six-minute segments). Tracks (x and y coordinates of each ant) were then imported into MATLAB to extract the various activity parameters before statistical models were implemented. Tracks were smoothed using a 10th order median filter and sections of continuous tracks less than 5 frames long (0.2 seconds) were excluded from activity calculations. Only ants that travelled from one side of the bridge to the other were included in the analysis and times when ants went underneath the bridge were excluded. The activity parameters of interest were speed travelled, variation (standard deviation) in speed per ant, proportion of time spent stationary per ant and the path tortuosity. The speed of an ant in each frame was calculated as the displacement in the ants' position between two consecutive frames, as in previous chapters. The median speed was then calculated for each individual. The proportion of time the ants spent stationary was calculated as the proportion of time the ant was travelling at less than 2 mm s^{-1}. Frames where the ants were found to be stationary were removed from the calculations of the ants' speed. Finally, I explored if noise affects the tortuosity or 'directness' of the ants paths. Tortuosity was calculated as the length of the most direct path the ants could have taken between their start and end point divided by the sum of the total distance travelled between these points. This gives a value between 0 and 1, with 1 being the most direct possible path and values closer to 0 being more tortuous paths. The tortuosity data had a very strong left skew due to the majority of the ants' paths being very straight, likely due to the narrowness of the bridge they were crossing. Therefore, I examined how the proportion of ants with paths greater than 0.85 tortuosity varied with the noise level. I also explored how the level of ant traffic changed over time. I did this by measuring the cumulative movement of ants both towards and away from the food source using manually scored data from BORIS (see next paragraph). This was calculated by binning the data into 4 second increments and then increasing the cumulative number of ants by one whenever an ant appeared on the bridge. This was explored for ants travelling towards and away from the food source separately.

Pheromone laying dynamics - To explore how the ants' laying rate varied in different levels of noise, I scored the lateral videos (Figure 5.1b) using BORIS (Friard and Gamba, 2016). Ants were given an individual ID and scoring information included the time at which an individual ant entered and exited the bridge and from which side, whether the ant went under the bridge (as these times were excluded) and the frames when they were laying pheromone. All events were recorded as state events. Pheromone laying was defined as when the ants gaster curved downwards and was touching the surface of the bridge. This method has been used to measure pheromone laying in previous studies (Beckers et al., 1992*a*; Jones et al., 2019), however most previous studies observe discrete 'taps' on the ground while others observe 'streaks'. I observed both, so to standardise laying rates I used the total time with the gaster touching the ground. The trial was split into three sections, with 20 ants sampled for each section. The first section of the trial was made up of the first ten ants to enter from the left side of the bridge and the first ten from the right side of the bridge. Similarly the last section of the trial was made up of the last ten ants to enter from the left and right side of the bridge. The second or middle section comprised the first five ants entering from the left and right of the bridge both before and after the midpoint of the trial. This gave a total of 60 ants sampled for each trial, spread evenly across the three time-points.

5.2.4 Experiment 2 - Double bridge

To test if ants rely more or less on pheromone trails in different levels of visual noise, a double bridge choice experiment was used. The initial set-up for the experiment contained a plastic platform (72cm in length) leading to a food source of honey water (50% v/v) referred to as the 'long bridge' (Figure 5.2a). In the first phase of the experiment, ants were allowed to forage along this bridge for one hour, depositing pheromone as they forage, leaving behind a trail. No noise was projected during this phase. These ants were then all removed from the experimental arena and returned to the original colony. For the second phase of the experiment, a 'short bridge' (28 cm in length) was added as an alternative route, and one of three light treatments was projected into the arena - uniform light, low noise or high noise (Figure 5.2b). The same projector and light settings were used as in the first experiment. A new sub-colony of ants from the same colony was then introduced into the arena and allowed to forage, giving them the choice of using the shorter more efficient route, or the longer route containing the pheromone trail. Ants were allowed to forage for one hour. Each replicate was recorded from above with a Panasonic DMC-

GH4 DSLR camera equipped with a Panasonic Lumix G 14-42mm lens. The camera recorded in 4K resolution at 24 frames per second. Five replicates using different colonies were completed for each noise level. Once a replicate was completed, workers were returned to their original colony.

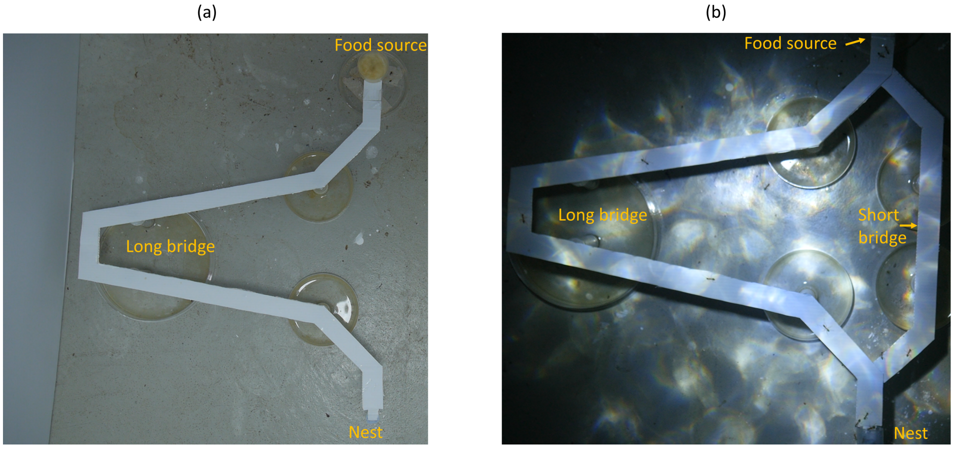


Figure 5.2: Set-up for the double bridge experiment. a) Set up for the first phase of the experiment where ants were allowed to lay a pheromone trail on the long bridge while foraging. No noise is projected during this phase b) Set-up for the second phase of the experiment where ants were given the choice between the long bridge containing the pheromone trail and the short bridge. In this phase different noise treatments were projected.

In order to determine the number of ants choosing either route, videos were scored using BORIS (Friard and Gamba, 2016). Every time an ant crossed the midpoint of each bridge, this was scored as an event. This data was then binned into 30 second bins and the proportion of ants on each bridge over time, under differing noise levels, was calculated.

5.2.5 Statistics

All statistics were performed in R 3.5.1 (R Core Team, Version 3.5.1). The package glmmTMB (Brooks et al., 2017) was used for all generalised mixed models and lme4 (Bates et al., 2015) for all linear mixed models. The dispersion and distribution of residuals was checked for all models and generalised linear mixed models (GLMMs) were checked using the DHARMa package (Hartig, 2019). Model comparison was done using the Anova function in the car package in R (Fox and Weisberg, 2019). A Type 2 Anova was run with the Chi-squared test statistic to test for significance of the fixed effects. Any non-significant effects were removed from the model before final analysis. All R graphs were created using *ggplot2* (Wickham, 2016).

5.2.5.1 Experiment 1 - Pheromone laying

Movement metrics – To explore how the activity levels of the ants varied with noise and direction the ants were travelling in, I first looked at how the speed of the ants varied in different levels of noise. The median speed for each individual was log transformed due to a positive skew and used as the response in a linear mixed model. Noise level was added as a fixed effect along with time (1-3), direction and the median number of ants on the bridge as ants could slow down to avoid collisions in high amounts of traffic. Trial was added as a random intercept. All activity models would not converge when adding trial nested within colony as a random intercept and therefore trial was used as the only random intercept in the activity statistics. I next investigated how the variation in ant speeds was influenced by noise. Standard deviation in speed was added as the response variable in a linear mixed model with noise and time as fixed effects. Trial was added as a random intercept and the response variable was square root transformed due to some positive skew. I also measured the proportion of time spent stationary by the ants. I again used a linear mixed model to test if noise impacted the proportion of time the ants spent stationary on the bridge. Proportion of time stationary was log transformed due to positive skew, noise level was added as a fixed effect along with time and the median number of ants on the bridge. The binary variable quantifying the proportion of ants with > 0.85 tortuosity was added as the response variable into a linear mixed model along with noise, time and the median number of ants on the bridge as fixed effects and trial as a random intercept. Finally, to investigate how the cumulative number of ants varied with noise, linear mixed models were implemented to look at the effect of noise and time on the movement in each direction separately. The interaction between noise and time was added as a fixed effect for both models along with trial as a random intercept. The number of ants entering on one side and exiting from the other was almost identical, therefore for the linear models I only modelled the number of ants entering from one side and travelling either towards the food or nest as the response variable in two separate linear mixed models.

Pheromone laying dynamics - I next explored the effect of noise on the pheromone laying behaviour of the ants. I first created a binary variable to define whether an ant laid (1) or did not lay pheromone (0) at any point in the trial. To do this I fitted a generalised linear mixed model (GLMM) with binomial error family with noise interacting with time in the trial (1-3) as a fixed effect along with the direction of travel (to or from the food source). Trial nested within colony was included as a random intercept. I next looked at the laying behaviour as a function of noise for only those ants that did lay. I did this by looking at the laying rate (proportion of time spent laying) for each trial. I fitted a GLMM with zero-inflated negative binomial error family due to the large number of low values in the data. The laying rate was multiplied by 100 and rounded to integer values to provide the response variable. The interaction between noise and time was included as a fixed effect along with the direction travelled. Trial nested within colony was included as a random intercept.

5.2.5.2 Experiment 2 - Double bridge

In order to determine whether the proportion of ants on each bridge differed with noise treatment, I used a binomial GLMM with the response being the combined values of the number of ants on the long and short bridge taken from the 30 second bins (i.e. cbind (number of ants on long bridge, number of ants on short bridge)). The interaction between noise and time was included as a fixed effect along with trial as a random intercept.

5.3 Results

5.3.1 Experiment 1 - Pheromone laying

Movement metrics

Noise had no influence on the median speed of the ants (Figure 5.3a; LMM; $\chi^2 = 0.98, df = 3, p = 0.81$). There was also no effect of time (Figure 5.3a; LMM; $\chi^2 = 0.13, df = 1, p = 0.72$) or direction (Figure 5.4a, LMM; $\chi^2 = 0.42, df = 1, p = 0.52$) on the median speed of the ants but ants did travel slower when greater numbers of ants were present on the bridge (LMM; $\chi^2 = 37.8, df = 1, p < 0.001$). Noise had no effect on the standard deviation of ant speed (Figure 5.3b ;LMM; $\chi^2 = 2.30, df = 3, p = 0.51$), and neither did direction (5.4b, LMM; $\chi^2 = 0.09, df = 1, p = 0.77$). However ants did show a greater variation in speed over time (Figure 5.3b; LMM; $\chi^2 = 38.2, df = 1, p < 0.001$) and less variation with a greater median number of ants on the bridge (LMM; $\chi^2 = 8.66, df = 1, p = 0.003$).

Noise had no influence on the proportion of time the ants spent stationary (Figure 5.4c; LMM; $\chi^2 = 3.62, df = 3, p = 0.31$) and neither did ant number (LMM; $\chi^2 = 0.30, df = 1, p = 0.58$). However ants did spend less time stationary later in the trial (Figure 5.4c; LMM; $\chi^2 = 27.8, df = 1, p < 0.001$) and less time stationary when returning to the nest (Figure 5.4c; LMM; $\chi^2 = 4.73, df = 1, p = 0.03$).

Neither noise nor time had an impact on the proportion of ants travelling in direct paths (Figure 5.3d; Noise effect: LMM; $\chi^2 = 0.60, df = 3, p = 0.90$; Time effect: LMM; $\chi^2 = 1.11, df = 1, p = 0.29$). A lower proportion of ants did, however, have more direct paths when there was a higher average number on the bridge (LMM; $\chi^2 = 26.4, df = 1, p < 0.001$) and when travelling back to the nest (Figure 5.4d; LMM; $\chi^2 = 5.08, df = 1, p = 0.02$)

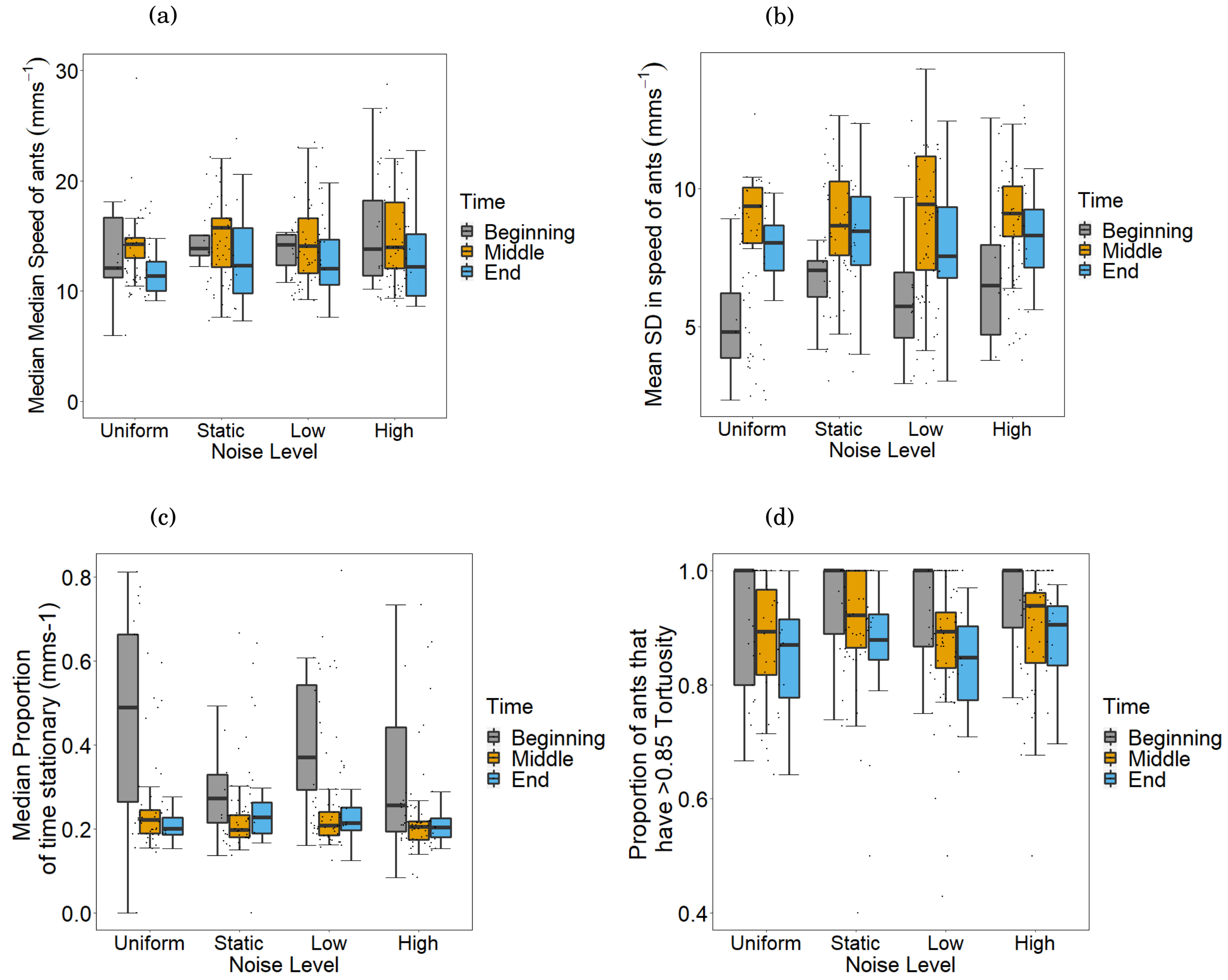


Figure 5.3: Ants activity levels do not change across noise levels but can vary with time. a) Median speed of the ants taken for each individual and then across each time period within a trial. b) Median standard deviation of the ants speed taken across each time period within a trial. c) Median proportion of time the ants spent stationary taken across each time period within a trial. d) Proportion of time the ants had a tortuosity greater than 0.85 taken across each time period within a trial. The central line of each box shows the median value while the upper and lower lines of the box show the upper and lower quartiles of the data. The whiskers extend to the data points within 1.5 × the interquartile range. Jittered points represent raw data points.

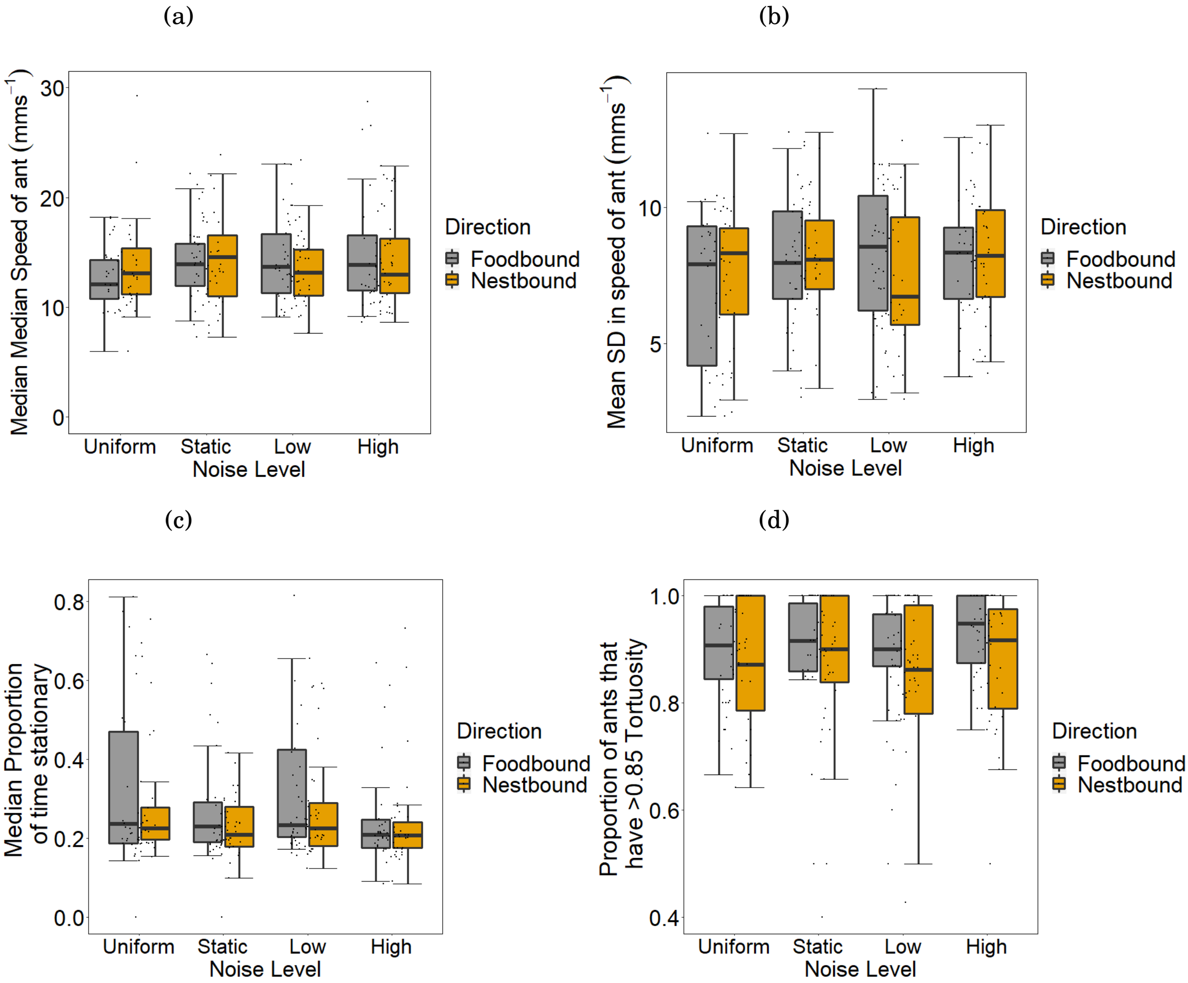


Figure 5.4: How the activity levels of the ants vary with noise and travel direction. a) Median speed of the ants taken for each individual and then across each time period within a trial. b) Median standard deviation of the ants speed taken across each time period within a trial. c) Median proportion of time the ants spent stationary taken across each time period within a trial. d) Proportion of time the ants had a tortuosity greater than 0.85 taken across each time period within a trial. The central line of each box shows the median value while the upper and lower lines of the box show the upper and lower quartiles of the data. The whiskers extend to the data points within 1.5 × the interquartile range. Jittered points represent raw data points.

The cumulative movement of ants varied across noise levels and over time. The total number of ants moving towards the food was higher than the movement of ants towards the nest (Figure 5.5). The number of ants entering on one side and exiting on the other side of the bridge was almost identical (Figure 5.5). There was an interaction between noise and time, with the cumulative number of ants moving towards the food source increasing most steeply in low noise followed by uniform light, with high and static noise levels having the smallest increase in the cumulative number (Figure 5.6a; LMM; $\chi^2 = 1102.8, df = 3, p < 0.001$). The cumulative number of ants moving towards the nest showed similar results with the cumulative number increasing most steeply in low noise followed by uniform light (Figure 5.6b; LMM; $\chi^2 = 1150.4, df = 3, p < 0.001$). Predicted figures with the raw data can be seen in Figure 5.7. Overall however, there did not appear to be a systematic effect of noise on the number of ants either moving towards or away from the food source.

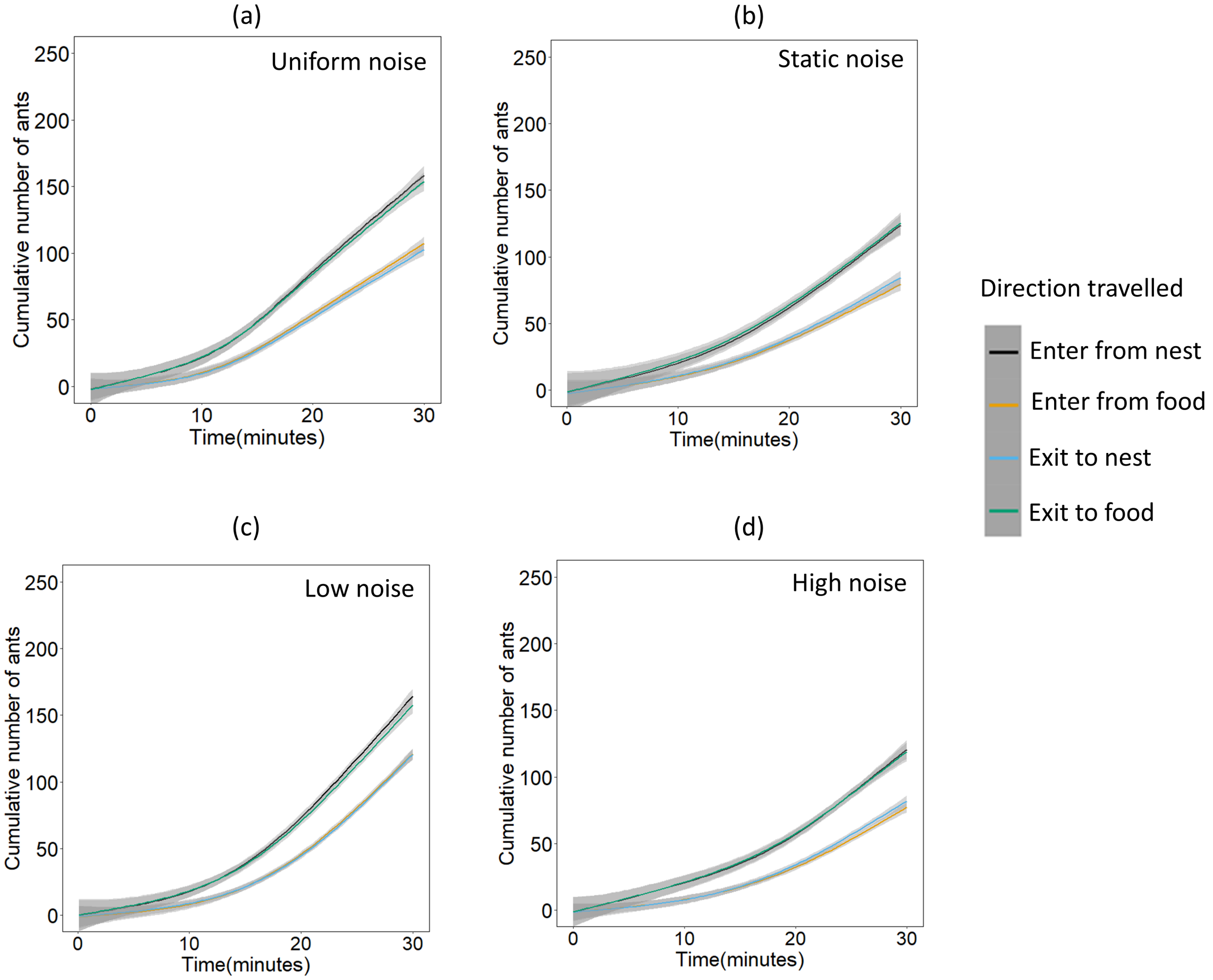


Figure 5.5: The cumulative movement of ants in different noise levels using four different measures. Enter from the left and exit from the right are both measures of movement towards the food source and enter from the right and exit from the left are both measures of movement towards the nest. a) The cumulative movement of ants in uniform light, b) in static noise, c) in low noise d) and in high noise. Plots are made using the raw data and smoothed across times within trials for each noise level using the default 'gam' method in the *geom_smooth* function in ggplot2. Grey areas show the 95% confidence intervals for the smoothed raw data.

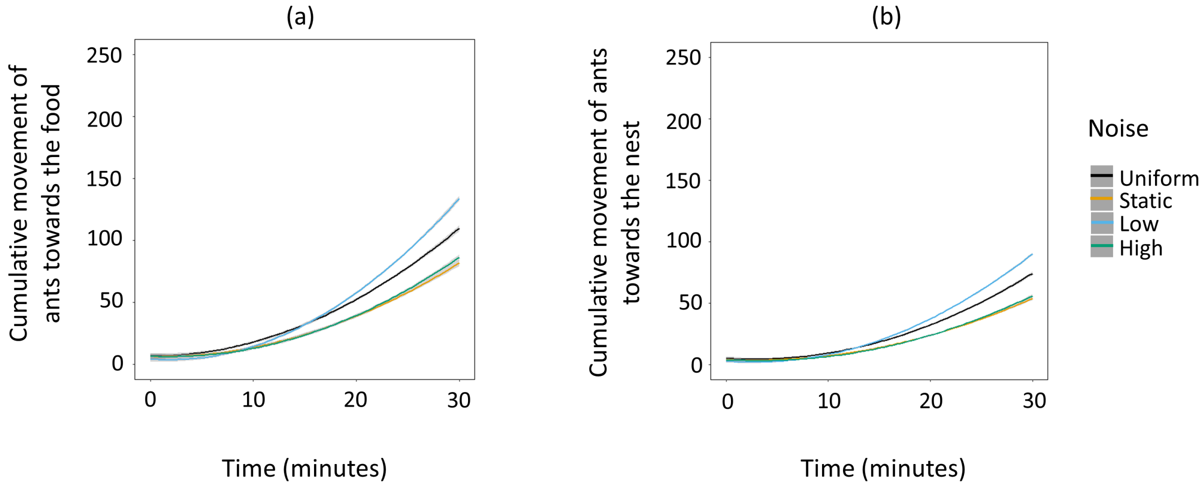


Figure 5.6: The predicted cumulative movement of ants in different levels of noise and when foraging both towards and away from the food. a) Predicted movement towards the food source. b) Predicted movement towards the nest. Plots are based on the statistical model predictions with each line showing a different noise level and smoothed across times within trials using the 'lm' method. 95% confidence intervals for the predicted values are shown in grey.

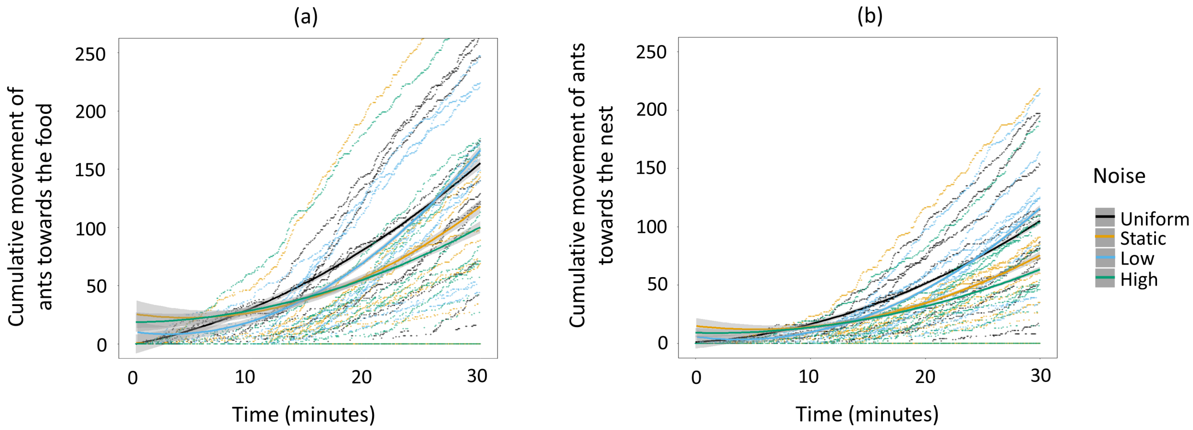


Figure 5.7: The cumulative movement of ants in different levels of noise and when foraging both towards and away from the food with the raw data plotted underneath a) Movement towards the food source. b) Movement towards the nest. Plots are using the raw data with each line showing a different noise level and smoothed across times within trials using the default 'gam' method in the geom$_smoothfunctioninggplot2$.

Pheromone laying dynamics

I then explored the impact of noise, direction and time on the binary effect of whether an ant lays pheromone or not, and then again as a function of the time spent laying in each of the two directions. First, a higher number of ants laid when returning from the food to the nest compared to those travelling towards the food (Figure 5.8a, $\chi^2 = 43.8, df = 1, p < 0.001$). Next, examining only the ants that did lay, I explored the proportion of time spent laying in each of the two directions.

Again, the ants spent a larger proportion of time laying when returning from the food to the nest compared to when travelling towards the food (Figure 5.8b, $\chi^2 = 8.77, df = 1, p = 0.003$). Next looking at the effect of noise and time, I found a significant interaction between noise and time on the proportion of ants laying (Figure 5.9a; $\chi^2 = 9.21, df = 3, p = 0.027$). In uniform, static and low noise levels, there was a negative trend, with a lower proportion of ants laying later in the trial. In high noise levels, however, a consistently high proportion of ants laid pheromone, even in the later stages of the trial (Figure 5.9a). Similarly, when looking at the proportion of time spent laying at different times in the trial, there was a significant interaction between noise and time (Figure 5.9b; $\chi^2 = 9.41, df = 3, p = 0.024$). In both uniform light and static noise, ants appear to lay less over the course of the trial, however in high noise levels, pheromone-laying ants laid more pheromone, especially in the middle section of the trial (Figure 5.9b).

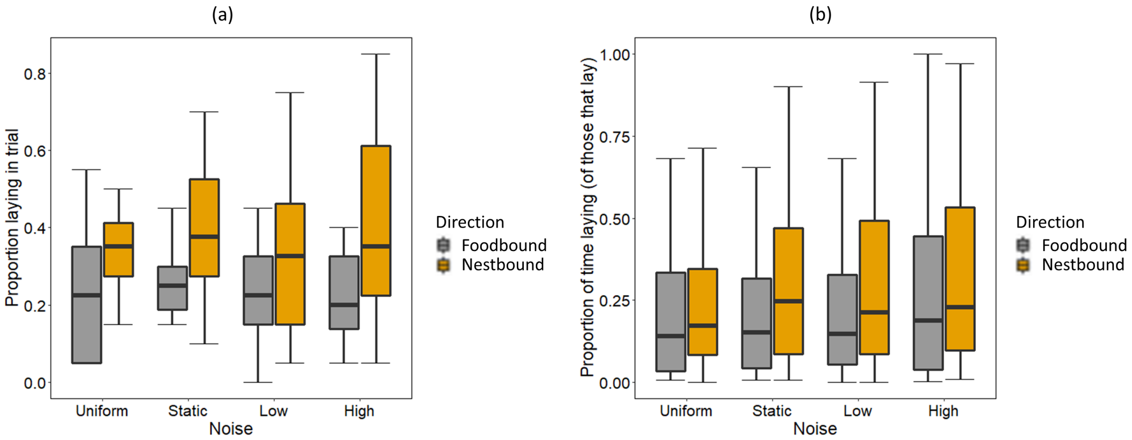


Figure 5.8: Pheromone laying behaviour in different levels of noise and in different directions. a) The proportion of ants laying in different noise levels and in each direction in each trial. b) The proportion of time laying for those ants that laid as a function of noise level in each trial. The central line of each box shows the median value while the upper and lower lines of the box show the upper and lower quartiles of the data. The whiskers extend to the most extreme data point within 1.5 × the interquartile range.

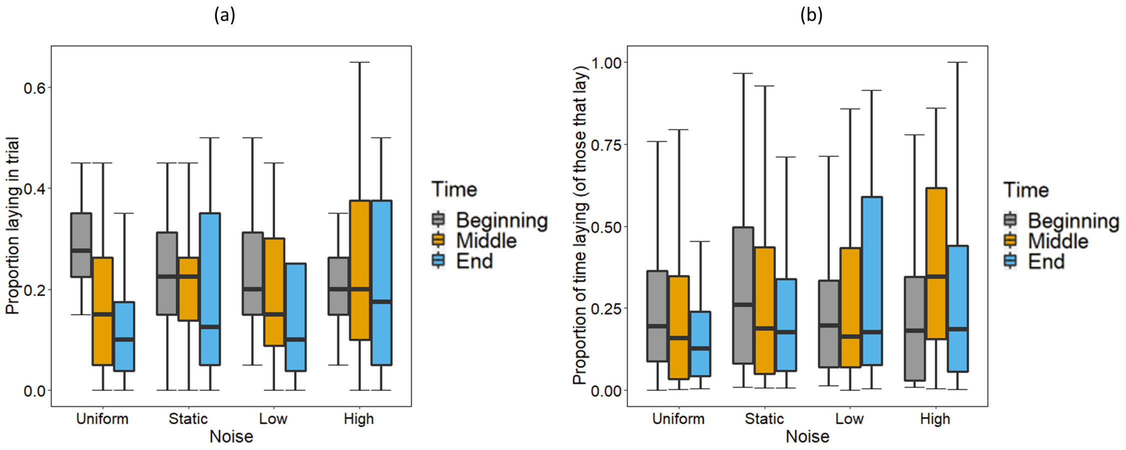


Figure 5.9: Pheromone laying behaviour in different levels of noise across different times in the trial. a) The proportion of ants laying in different noise levels and at different times (1 to 3) in each trial. b) The proportion of time laying for those ants that laid as a function of noise level and time (1 to 3) in each trial. The central line of each box shows the median value while the upper and lower lines of the box show the upper and lower quartiles of the data. The whiskers extend to the most extreme data point within 1.5 × the interquartile range.

5.3.2 Experiment 2 - Double bridge

When exploring whether ants chose the long bridge containing a pheromone trail or the shorter bridge, I found a significant interaction between noise and time on the proportion of ants on each bridge (Figure 5.10; GLMM; $\chi^2 = 13.1, df = 2, p = 0.0014$). While in all noise treatments, the number of ants using the shorter bridge increased over the course of the trial, ants took longer to switch to using the shorter bridge in higher levels of noise (Figure 5.10).

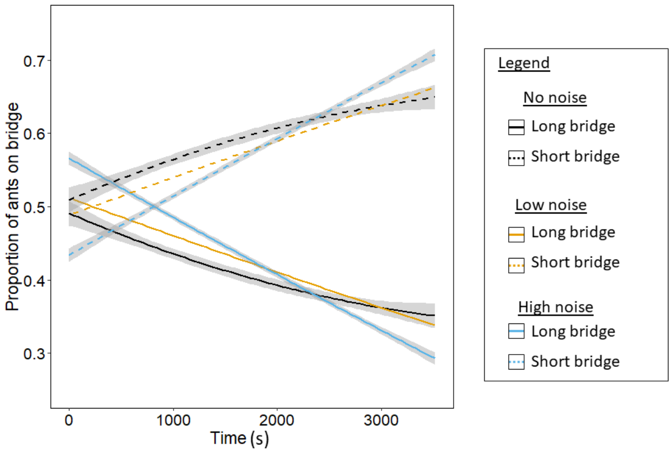


Figure 5.10: The predicted proportion of ants on the long (solid lines) and short bridge (dashed lines) over time and in different levels of noise. Black lines are for no noise treatments, orange for low and blue for high noise. The predicted data are taken from the model predictions and smoothed across times within trials using the ‘lm’ method in the *stat_smooth* function in ggplot2. Grey shaded areas show the 95% confidence intervals from the model predictions. Note the scale on the y axis has been zoomed in.

5.4 Discussion

In this chapter, I first explored whether visual noise affects the pheromone laying behaviour and activity levels of weaver ants while foraging. I found little evidence to suggest that ants are varying their activity in different noise levels and no clear evidence of their cumulative traffic flow being affected by noise. However, ants laid pheromone more consistently over time in higher levels of noise. Furthermore, when given a choice between a long bridge containing social information (a pheromone trail) and a shorter more efficient route, ants were collectively quicker to choose the shorter route in the lower levels of noise.

I found little evidence for ants changing different measures of activity in noise. Although it appears from Figures 5.3a and 5.3d that ants are slowing down later in the trial and are travelling in less direct paths, this was explained by the amount of traffic on the bridge. The amount of traffic increased later in the trial which is likely due to increased recruitment of foragers (Chadab and Rettenmeyer, 1975; Hölldobler et al., 1990). This in turn led to the ants slowing down and travelling in less direct paths to avoid collisions with the greater number of ants on the bridge. In contrast, I found that ants spent less time stationary later in the trial once the number of ants on the bridge is taken into account. This may be due to ants being more reliant on the established pheromone trail later on in the trial and therefore more certain about what direction to travel in, as the probability of an ant following a trail is based on the concentration of pheromone on that trail (Pasteels et al., 1986). Because the pheromone trails are informing the ants that they are on the correct path, this should have lead to less pausing and error checking as the trial progressed (Czaczkes et al., 2011). Ants also spent less time stationary when returning to the nest, likely because they have a strong objective of returning food to the nest and recruiting more foragers. However, ants appeared to have less direct paths when returning to the nest, although this could be because of the increased number of foragers travelling towards the food source against their direction of movement, resulting in returning ants turning to avoid this traffic in order to avoid collisions (Couzin et al., 2003; Dussutour et al., 2004). Individual ants had a lower variation in speed with a greater number of individuals on the bridge. Ants would be more likely to collide with each other when in greater numbers meaning they would have less capacity to reach greater speeds. This could in turn limit the amount of variation in an individuals speed. Conversely ants showed a greater variation in speed over time. Perhaps the pheromone laying was homogenising their movement - when laying pheromone the ants appeared to be travelling at a more consistent speed. Therefore as the amount of pheromone reduces over time in most noise treatments, this could lead to a greater variation in speed over time. However this result still holds for high noise where pheromone laying does not decrease over time.

Noise did not appear to affect the overall ant traffic movement measured by the cumulative number of ants on the bridge in each direction. Although there was a difference in the slopes of the cumulative movement of ants with noise, it did not appear to be a large difference or vary with noise in a systematic way. Furthermore, the variation in cumulative movement between trials is very large and therefore this difference between slopes could be due to this large variation. Because the number of ants travelling from the nest was always higher than the number returning from the food in all times of the trials, this suggests that across all treatments, the ants were still in the recruitment phase of foraging meaning that the behaviour of ants was comparable across trials. Overall, the ants appeared robust in their foraging rates in different levels of noise.

The overall lack of effect of noise on ant activity could be due to one of two reasons. Either the ants did not perceive the noise, or they have adaptations to mitigate the effects of noise. Since noise had a significant effect on aspects of the ants laying behaviour (see below), it is highly unlikely that they are not perceiving the noise, so mitigation is almost certainly taking place. One possible adaptation could be that the ants' pheromone laying was compensating for their possible reduction in visual perception. *Lasius niger* ants increase pheromone laying after experiencing a change in the location of their food source (Czaczkes et al., 2013; Czaczkes and Heinze, 2015). Ants could therefore increase deposition in perceptually challenging environments to aid other colony members when visual cues are less certain. Second, another adaptation could be the ability of ants to detect polarised light (Jander and Jander (1998) and reviewed in Zeil et al. (2014)). If the ants were seeing the polarised light in a separate visual channel, they could choose to place more reliance on this channel. Nocturnal bull ants (*Myrmecia midas*) can decide whether they place more reliance on terrestrial or polarisation cues depending on context (Freas et al., 2017). The weaver ants here did not appear to be alarmed by the noise, as their alarm response is to spray alarm pheromone and adopt a characteristic aggressive posture (gaster raised and mandibles flared (Hölldobler et al., 1990)), which is not something I observed. Therefore it is likely that the presence of pheromones as an alternative sensory channel was at least partly compensating for the visual disturbance which could explain why the ants activity was consistent.

The proportion of ants laying appeared to be more consistent over time in high noise levels compared to the other noise treatments where laying rates decreased over time. The proportion of time spent laying (of those ants that did lay) was also more consistent across time in the high and low noise treatments compared to the static and uniform, where the laying rate decreased over time. Therefore, whereas in low or no noise treatments ants stopped laying as the pheromone trail became saturated, in higher noise they continued to lay over time. This indicates that ants are in fact perceiving the visual noise due to this behavioural change. If the ants are being negatively impacted by noise and are less certain about their route, they could therefore become more reliant on the pheromone trail compared to their vision in the visually noisy conditions. In low light environments *Lasius niger* ants lay more pheromone and are more likely to follow these trails (Jones et al., 2019) which is likely due to the reduction in visual perception that they are experiencing. In my experiment the ants were maintaining their laying rates over time in higher noise conditions. This would mean that because the ants have the option to choose to follow this pheromone trail and not just rely on vision, they are behaviourally robust to visual noise. In my experiment the proportion of ants laying and proportion of time laying was also higher when returning from food compared to travelling towards the food. This is expected as once the ants know about the location of the food source, they have more reason to lay pheromone to guide others to that location (Czaczkes and Heinze, 2015).

I show that ants lay more pheromone in higher noise levels, but did they choose to rely on pheromone more? When given a choice between a long bridge containing social information and a shorter more efficient route, the proportion of ants on each bridge changed over time and in different levels of noise. When there was no noise projected there was approximately a 50% chance that ants would choose either bridge at the start of the trial before the proportion on the short bridge gradually increased over time. This is perhaps surprising as it would be expected that the majority of ants would follow the pheromone trail at the start of the trial before individuals have had a chance to explore, even in the no noise treatment, as it is widely known that many ants use pheromones to guide nest-mates to food sources (Hölldobler et al., 1990; Sumpter and Beekman, 2003). Therefore without any noise stimulus present, it would be expected that the ants default choice would be the pheromone trail. If the ants could see the food source from their starting position by the nest however, this could explain why half chose to take the more direct route. Argentine ants (*Linepithema humile*) significantly prefer straighter routes with the fewest number of turns (Yates and Nonacs, 2016). The number on the shorter bridge could also be because the ants viewed the short bridge as unmarked territory and therefore were motivated to explore and mark this novel area that does not contain any pre-laid pheromone trails. Argentine ants choose random directions, independent of other foragers when encountering new terrain (Mahavni et al., 2019). The increase in ants using the shorter bridge over time is likely because as pheromone accumulated on the bridge, this in turn encouraged more ants to use this route and therefore more ants discovered its efficiency (Beckers et al., 1992*b*).

While in all noise treatments the number of ants using the shorter bridge increased over the course of the trial, ants took longer to switch to having the majority on the shorter bridge in high levels of noise, with those in low noise showing an intermediate effect. In the high noise treatment, more ants initially used the longer bridge compared to the short bridge, but this pattern is not observed in the no noise treatment. This could suggest that the visual noise was making it more difficult for the ants to perceive visual cues. Furthermore, when individuals are more uncertain about their environment, they can choose to copy others (Laland, 2004), which in this context could mean more ants choosing to rely on social information. Here, therefore, individual weaver ants could initially have chosen to rely on pheromone trails when in perceptually demanding visual environments due to the ‘copy when uncertain’ strategy. However this preference could also simply be because the ants had the option of choosing to use information in a different sensory modality to the visual noise. It could therefore make sense that individual ants would initially choose the information perceived in the modality different to the visual noise which is why here they choose the pheromone trail. Further experiments would be needed to separate this idea of using a different sensory modality with the ‘copy when uncertain’ strategy. Perhaps by having an extra treatment that uses a non-social food scent to replace the pheromone as a non-visual cue to the food source.

Taken together, it appears that ants may be increasing their reliance on social information in high noise due to their more consistent pheromone laying and larger initial preference for the pheromone trail in the double bridge experiment. Where previous experiments have tested how a reduction in visual perception affects ants’ reliance on pheromones outside of their normal circadian rhythm (Jones et al., 2019), I tested fluctuating light as it would appear beneath a tree canopy during their circadian day, which removes this potential confound. While it is almost certain that weaver ants perceive this visual noise, it appears these ants have mechanisms they can use to counteract the detrimental effects of noise in their environment. Living in arboreal habitats they are likely to experience dappled light often and therefore have adapted to cope with this. Pheromone trails are not affected by this visual noise and provide another sensory channel for the ants to use. Individuals can choose to copy others when uncertain about the nature of their environment (Laland, 2004), and therefore a change in the accuracy and reliability of information from personal vs social sources of information may lead individuals to switch the information source they use (Czaczkes et al., 2019). Hence in my experiments, individual weaver ants could have been choosing to increase their reliance on pheromone trails when in perceptually demanding visual environments.

CHAPTER 6

GENERAL DISCUSSION

6.1 Thesis summary

In this thesis, I have demonstrated the impacts that two forms of visual noise, water caustics and dappled light, have on the behaviour of two animal taxa. In Chapter 2, I found that water caustics with faster flicker speeds reduced the visual perception of sticklebacks (*Gasterosteus aculeatus*) and fish responded to this by selectively searching over more localised areas of their visual field. In Chapter 3, I explored the behavioural adaptations that these fish use to mitigate the impact of visual noise on their perception. I found that fish spent less time in more visually noisy areas of their environment, and achieved this by swimming faster and spending less time stationary in noisier areas. In Chapter 4, I explored whether sticklebacks had any social adaptations to mitigate the effects of increased noise. I found that fish became more correlated in their speed and swam closer together in higher levels of visual noise, but found no evidence that access to social information improved the fish's collective ability to detect prey in noisy conditions. In Chapter 5, I investigated how a different form of dynamic visual noise, artificial dappled light, affected social information use in weaver ants (*Oecophylla smaragdina*). The activity levels of the ants generally did not vary with noise level, and there was no difference in recruitment to food sources in different levels of noise. However, in the highest noise treatment, ants laid pheromones more consistently over time. Further, when given a choice between a longer route containing social information (the pheromone trail) and a shorter, more efficient route lacking these cues in different levels of noise, ants were quicker to choose the shorter route in lower levels of noise and took longer to switch to this route in the higher levels of noise. These results highlight that the ants appear to be more reliant on social information in higher noise levels, and this may compensate for any negative impacts imposed on them by noise. In this General Discussion, I discuss my findings in relation to visual adaptations to noise, changes in the visual noise environment, multi-sensory adaptations to visual noise and then explore some comparisons between visual and acoustic noise. I finish by outlining future work in this field.

6.2 Visual adaptations to noise

In this thesis, I largely focused on the impacts of visual noise on behaviour. It is also important to consider, however, the visual adaptations that some species may possess to mitigate the impacts of visual noise on perception. Indeed, in Chapter 2, I found that fish appeared to reduce the area of the visual field they scanned in higher levels of noise, which could ensure information is detected in those smaller regions, albeit at the expense of decreased coverage. How might fish selectively scan particular regions of their visual fields? Fish could achieve this by adjusting the position of their lens within their eye. Through muscular contractions, fish can view objects closer to themselves by moving their lens towards their cornea, and can view objects further away by moving their lens towards their retina in a process called accommodation (Bone and Moore, 2008). Therefore, perhaps in different levels of noise, fish can selectively change the size of their search area by actively shifting their lens. Such a response may ensure at least some prey are detected in the fish's visual field in times of increased noise. Testing this hypothesis could be achieved by measuring the lens position in a fish's eye using lasers (Fercher and Roth, 1986; Findl et al., 1998) and seeing how this influences detection of prey in different levels of visual noise.

In contrast to the visual system of fishes, ants have compound eyes made up of tens to hundreds of separate optical units, each equipped with its own lens and photoreceptors. The advantage of this type of eye is that it gives ants a wide field of view and depth of field, but these eyes are less sensitive to light, with spatial resolution limited by the number of optical units (Borst and Plett, 2013; Land and Fernald, 1992). Such reduced resolution may in fact mean that changes in light intensity, such as those caused by dappled light, may be largely filtered out during early stages of information processing. Indeed, spatial and temporal summation of noisy scenes could result in intensity-based noise being averaged over space or time, much like smoothing in signal processing (Stöckl et al., 2016). Therefore, through signal averaging, as a by-product of having lower resolution vision, signal to noise ratios could be increased, reducing the interference of visual noise in ants.

Other animals have visual adaptations to mitigate the impacts of visual noise on perception (Matchette, 2020). Fan worms (*Acromegalomma vesiculosum*) have eyes with a high temporal resolution which are ideally suited for filtering out high-frequency visual noise such as caustic flicker, while at the same time remaining sensitive to rapidly moving predatory threats (Bok et al., 2019). Furthermore, many cephalopod and crustacean species are sensitive to polarised light (Horváth et al., 2004), allowing individuals to utilise a different visual channel which is unimpeded by intensity-based visual noise (i.e. brightness) (Brayley et al., 2022). Indeed, fiddler crabs (*Uca stenodactylu*) use polarisation vision as this allows them to detect conspecifics or predators against the glare of the surrounding mud flats (How et al., 2015). While there is a wealth of literature on interspecific variation in eye morphology, exploring specific visual adaptations to different types of visual noise in the environment is worth investigating more extensively. This could include metanalyses that link particular sensory adaptations to particular types of noise.

6.3 Is visual noise changing in the environment?

In this thesis, I focused on naturally and ecologically relevant forms of visual noise - water caustics and dappled light - that animals will have been exposed to over their evolutionary history. Even so, I detected impacts of visual noise on prey detection, habitat selection, and social information use, highlighting that noise places constraints on perception, and animals have evolved strategies to mitigate these constraints. A key question, however, is whether these types of noise are likely to increase or decrease in frequency and intensity with environmental change. Indeed, species in urban environments where there is reduced vegetative cover may be exposed to less dappled light compared to more natural environments. Other forms of environmental change may either add to or reduce the impacts that these naturally occurring forms of visual noise have on animals. For example, climate change is leading to an increase in the severity of storms with greater turbulence, and higher turbidity in rivers from the increase in suspended sediment (Partan, 2017). Furthermore, an increase in agricultural run-off is leading to increased eutrophication in rivers and coastal darkening (Mustaffa et al., 2020; Newton et al., 2003). How reduced visibility interacts with water caustics to impact perception and behaviour has not been tested. Indeed, increased turbidity will reduce light penetration, which could reduce the intensity of caustic flicker, or alternatively could increase light scattering compounding the impacts of caustics on an animal's visual perception. Animals are likely experiencing change, therefore, in the types and amount of visual noise that is present in their habitats.

If animals are experiencing changes to visual noise in their environments, a key question is how they will adapt to such changes. In Chapter 3, I found a key behavioural response from the sticklebacks was to avoid areas of their environment with increased levels of visual noise. However, habitat degradation could make it more difficult for individuals to find refuges from noisy environments, and reduced connectivity between habitats (Beier et al., 2008; Forman et al., 2003) could further limit whether animals can avoid areas of increased visual noise. Therefore, animals may be less likely to be able to behaviourally mitigate the impacts of noise, and this reduction in an ability to detect information about prey or predators could have strong fitness consequences on individuals (Brumm and Slabbekoorn, 2005; Lowry et al., 2012; Siemers and Schaub, 2011). Noisy environmental conditions, therefore, could provide a platform for selection to act on the perceptual abilities of individuals in populations. Indeed, in environments with consistently high levels of noise, selection could act to improve an individual's perceptual abilities through increasing their sensing capabilities by increasing the number of sensors. Alternatively, selection could also act to reduce perceptual abilities in environments of increased noise. This could happen if noise in the environment were so extreme that additional investment in sensory machinery to compensate for such increases in noise became too costly, favouring reduced investment in sensory machinery and instead investment in other sensory channels or behaviours. Indeed, there is good evidence that environmental noise in acoustic channels is changing the way animals detect and communicate with one another. Great tits (*Parus major*), for example, choose to sing at higher frequencies (Slabbekoorn and den Boer-Visser, 2006) and choose songs out of their repertoire which are less likely to be masked by low pitched anthropogenic noise (Slabbekoorn and Ripmeester, 2008). Similarly, the male reed bunting (*Emberiza schoeniclus*) (Gross et al., 2010) and European robin (*Erithacus rubecula*) (McLaughlin and Kunc, 2013) can increase the minimum frequency of their calls in the presence of environmental noise. The vast majority of studies have focused on acoustic noise, and therefore a key future area of research would be to explore how visual noise, induced by environmental change, is affecting the physiology and behaviour of animal populations.

6.4 Cross-modal adaptations to noise

Throughout this thesis, I have largely focused on the visually guided behavioural responses of animals to visual noise. For example, in times of increased visual noise, I found that fish were less likely to detect virtual prey that were formed of only visual features, adapted their movements (a process which is largely visually guided (Rosenthal et al., 2015)), and adapted some aspects of their social coordination with conspecifics (again, primarily achieved through visual cues (Herbert-Read et al., 2015)). In Chapter 5, however, I explored how ants adapted non-visual aspects of their behaviour in the presence of visual noise. In particular, I showed that ants rely more on their pheromone trails in increased levels of noise. This is a rare example of a cross-modal adaptation to noise, where animals rely more on a different sensory modality to the source of noise. While there are relatively few examples of animals selectively switching to a sensory modality that is less impacted by noise, this strategy is likely to be common in nature. Indeed, animals often combine multiple modalities in their signals to conspecifics, for example including both acoustic and visual components. While it has been suggested that combining information from multiple modalities results in redundant information being conveyed to a receiver (Preininger et al., 2013), combining multiple cues could provide ways for animals to mitigate the impacts of noise on perception by providing information in an alternate sensory channel that may be less impacted by noise. Indeed, small torrent frogs (*Micrixalus saxicola*) call to conspecifics from streams where the acoustic noise from water is likely to impede communication. However, by using both visual and acoustic components in their courtship signals, signal detection does not appear to be constrained (Preininger et al., 2013). Therefore, animals appear to make use of multimodal cues to combat the negative impacts of noise, which, combined with sensory switching, could mitigate the perceptual constraints imposed by noise (Partan, 2017). It would be valuable to investigate further whether there are other forms of cross-modal adaptations that allow animals to adapt to noisy conditions.

6.5 Comparisons between visual and acoustic noise

While I solely explored the effects of visual noise in this thesis, a large proportion of previous research on noise has focused on acoustic forms. In Chapter 2 I found that fish were less likely to detect prey in visually noisy environments. Have similar findings been observed in acoustic noise conditions? Both overlapping and non-overlapping acoustic noise causes the number of successful prey localisations to half and the search time to nearly triple in pallid bats (*Antrozous pallidus*)

(Allen et al., 2021). Furthermore, three-spined sticklebacks (*Gasterosteus aculeatus*) that have been exposed to acoustic noise have an increased number of food handling errors and a reduced ability to discriminate between food and non-food items leading to a reduction in foraging efficiency (Purser and Radford, 2011). Similarly, shore crabs (*Carcinus maenas*) exposed to a ship noise playback are more likely to freeze during eating or move away from food than when exposed to an ambient noise playback (Wale et al., 2013). Therefore both acoustic and visual noise can reduce the foraging efficiency of individuals.

In Chapter 3 I found that fish avoided more visually noisy areas of their environments. Animals can also choose to avoid acoustically noisy environments. Indeed, acoustic noise leads to avoidance behaviour in zoo animals. Elephants move into quieter areas when exposed to continuous acoustic noise and giraffes move into quieter locations when exposed to intermittent acoustic noise (Jakob-Hoff et al., 2019). Similarly, recordings of traffic noise lead to a decline in abundance, and in some cases almost complete avoidance, by several bird species along experimentally produced noise corridors simulating roads (McClure et al., 2013). This is likely due to the birds' inability to pick up on other sounds such as the songs of conspecifics or predators, or could also be due to stress caused by the loud noise (Slabbekoorn and Ripmeester, 2008). Therefore animals can choose to avoid noise in acoustic as well as visually noisy environments.

In Chapter 4 and 5 I explored whether there were any social adaptations to visual noise. I found that pairs of fish change some aspects of their cohesion and coordination in visually noisy environments. Similar to this, acoustic noise reduces the spatial and directional organisation of juvenile seabass shoals (*Dicentrarchus labrax*), causing them to become less cohesive and less directionally ordered (Herbert-Read et al., 2017). In both cases, this could be an adaptation to improve access to social information in noise which is also consistent with what I found in Chapter 5 with the ants. There are very few studies that explore social adaptations of groups to environmental noise so this would be a valuable avenue for future research.

6.6 Outstanding questions

In this thesis, I have explored the impact of natural forms of visual noise on animal behaviour and perception and while it has also been well documented that animals change their behaviour in response to acoustic noise (Kunc et al., 2016; Shannon et al., 2016), the impacts of other forms of noise in other sensory channels have been less well investigated. Investigating a broader range of forms of noise across a larger variety of taxonomic groups would reveal the general principles of how animals adapt their cognitive and behavioural strategies in response to noise. In particular, studies focusing on different forms of chemical (Raguso, 2003) or mechanical noise (Roberts and Laidre, 2019) would be particularly worthwhile. As described above, studies investigating the cross-modal effects of noise are also rare (Chan et al., 2010), as well as studies that examine multiple sources of environmental noise in combination (Ginnaw et al., 2020). Exploration of how responses to noise could be intensified by additional environmental stressors that do not directly affect environmental noise, such as changing temperatures or ocean acidification having effects on physiology (Clark et al., 2020), would also be worthwhile.

More studies that measure the responses of individuals over a gradient of noise levels would also be valuable instead of solely comparing high and low noise intensities (Gomes et al., 2021). Many studies, for example, simply measure the presence or absence of noise on behaviour, and this may miss the subtleties of behavioural or sensory modifications to noise. For example, anti-predator behavioural responses in western mosquitofish (*Gambusia affinis*), were greatest when fish were tested at an intermediate level of turbidity, while there was no difference in behaviour between the clear and high turbidity treatments (Ehlman et al., 2019). Similarly, low frequency acoustic noise can have stronger effects on the shoaling behaviour of European minnows (*Phoxinus phoxinus*) than high frequency noise (Currie et al., 2021). Assessing how different intensities, frequencies, or exposure times impact organisms is important for understanding how sensory systems are tuned to ecological conditions, and the impact that different forms of anthropogenic noise may have on these organisms.

Longer term studies investigating the effects of noise are also rare. Measuring the impacts of noise on populations over generations could give insight into how species adapt to noise over ecological and evolutionary time scales. For example, guppies (*Poecilia reticulata*) experimentally raised in turbid water demonstrate developmental plasticity in opsin gene expression in a manner that is likely to improve the detection of moving objects when visual information is limited in turbid water (Ehlman et al., 2015). In other cases, if some species cannot adapt to increased noise levels (e.g. turbidity levels), this could lead to changes in species assemblages (Ehlman et al., 2020; Witte et al., 2013) and affect speciation processes (Seehausen et al., 1997). Habitat dependent ambient noise has been shown to create a selection pressure on the calls of the little greenbul (*Andropadus virens*). This selection pressure causes both acoustical (e.g. minimum and maximum frequency of songs) and morphological traits to diverge, which the authors suggest could eventually lead to assortative mating and eventually to reproductive isolation (Slabbekoorn and Smith, 2002). Similarly the songs of urban great tits (*Parus major*) across Europe have diverged from nearby forest birds (Slabbekoorn and den Boer-Visser, 2006), showing that environmental noise can create long term impacts on species and populations. Exploring how a reduction in noise affects individuals with long term noise exposure could also provide knowledge on how systems recover from long term exposure. Finally, quantifying levels of different kinds of noise in natural environments would be a vital area of further research, building upon the work that has already been performed on measuring the frequencies of acoustic noise (Gomes et al., 2021). This should include how different forms of noise vary over different temporal and spatial scales, as this alters the effectiveness of different strategies to mitigate the effects of noise. For example, an infrequent, localised and intense source of noise may be more easily responded to with a behavioural response, while continuous exposure of less intense noise may favour modification of sensory systems over developmental or evolutionary time, even though the average level of noise over time and space may be similar. Such a foundation will allow future experiments to test predictions over ecologically-relevant levels of noise.

6.7 Conclusion

I have presented evidence that noise impacts the perception of individuals across two different systems, but that in both cases, individuals and groups have behavioural adaptations to mitigate these impacts. Animals live in inherently noisy environments with not only many natural forms of noise, but also increasing levels of noise from anthropogenic sources. Therefore understanding the behavioural and sensory adaptations animals have developed to deal with noise will allow us to understand how selection has shaped these processes and how best to reduce our impact on them.

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