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The effects of predator personality and cognition on predator-prey interactions

Andrew W. Szopa-Comley

Pike cichlids (*Crenicichla frenata*)
Photographs: A. W. Szopa-Comley

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Abstract

Predators and prey are engaged in a struggle for survival, in which both parties impose strong selective pressure on one another. To combat the catastrophic risk posed by predation, prey have evolved a range of adaptations designed to minimise the probability of being encountered, detected or captured by predators, including flexible behavioural responses. The success of predators in capturing prey is also profoundly influenced by the properties of individual predators, including their behavioural traits and cognition. In particular, consistent inter-individual differences in predator behaviour, or predator personality, have the potential to shape the behavioural decisions of predators at multiple stages of their interaction with prey, ultimately affecting the level of predation risk facing prey. In this thesis, I explore the effects of predator personality and cognition on predator-prey interactions, by studying three species of freshwater fish: three-spined sticklebacks (*Gasterosteus aculeatus*), pike cichlids (*Crenicichla frenata*) and blue acara cichlids (*Aequidens pulcher*). In Chapter 2, I begin by examining the effect of the bold-shy behavioural axis on the capacity of individual three-spined sticklebacks to detect prey. In Chapter 3, by presenting wild pike cichlid predators with a prey stimulus in their natural environment, I then explore the relationship between the factors influencing encounter rates and inter-individual variation in the response of predators to their prey. Next, in Chapter 4, I investigate how prey adjust their anti-predator behaviour following exposure to individual pike cichlids with contrasting personalities. Finally, in Chapter 5, I develop an experimental system in which real blue acara cichlid predators interact with robot-controlled prey, in order to test the effect of unpredictable prey escape tactics on learning by predators. Overall, my research points to the limitations of boldness in capturing the risk individual predators pose to prey, thus emphasising the importance of considering inter-individual variation in ecologically relevant behavioural traits.

Dedication and Acknowledgements

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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: DATE:

Contributions to chapters in this thesis which have previously been published:

Chapter 2. An adapted version of this chapter has been published in the journal *Behavioral Ecology and Sociobiology*:

Szopa-Comley, A. W., Donald, W. G. and Ioannou, C. C. (2020) 'Predator personality and prey detection: inter-individual variation in responses to cryptic and conspicuous prey', *Behavioral Ecology and Sociobiology*, 74, 70. doi: https://doi.org/10.1007/s00265-020-02854-9

I led the writing of the paper, conducted experimental trials, analysed videos and undertook the statistical analyses, with input from my supervisor Christos C. Ioannou. William G. Donald conducted experimental trials and analysed videos, as part of his undergraduate research project.

Chapter 3. An adapted version of this chapter has been published as a pre-print on *bioRxiv* and in the journal *Animal Behaviour*:

Szopa-Comley, A. W., Duffield, C., Ramnarine, I. W. and Ioannou, C. C. (2020) 'Predatory behaviour as a personality trait in a wild fish population', *Animal Behaviour*, 170, pp. 51-64.
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Szopa-Comley, A. W., Duffield, C., Ramnarine, I. W. and Ioannou, C. C. (2020) 'Predatory behaviour as a personality trait in a wild fish population', *bioRxiv*, 2020.06.19.161968.
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I designed the study, carried out data collection, analysed video recordings, conducted the statistical analysis and wrote the paper, in discussion with my supervisor Christos C. Ioannou. Callum Duffield and Indar W. Ramnarine assisted with data collection in the field.

Additional contributions to other chapters in this thesis:

Chapter 4. Jake Cush and Maria Sarju assisted with collection of wild fish from the field and helped to set up the pools used in the experiment.

Ethical approval:

Ethical approval for the experiments presented in this thesis was granted by the University of Bristol: project number UB/16/047 applies to Chapters 2 and 5; project number UB/17/006 corresponds to Chapters 3 and 4.

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Chapter 1:

General introduction

Images of some of the predatory fish species studied in this thesis:
one blue acara cichlid (*Aequidens pulcher*) above, and two pike cichlids (*Crenicichla frenata*) below.
Photographs: A. W. Szopa-Comley.

1.1 Introduction to predator personality and cognition

In response to the strong selective pressure imposed by predators, prey species have evolved a multitude of defensive strategies to maximise their chances of evading capture (Krause and Ruxton, 2002; Ruxton *et al*., 2004). At the same time, predators must ultimately overcome these defences in order to survive, triggering a dynamic struggle between predators and prey, which can have far-reaching consequences for entire ecosystems (Baum and Worm, 2009; Schmitz, Hawlena and Trussell, 2010; Estes *et al*., 2011).

Predator-prey interactions can be broken down into a sequence of events, starting with the initial encounter between a predator and its prey, and culminating in the eventual capture and consumption of prey by the predator, or a successful escape by the prey (**Fig. 1.1**). The probability of each successive event is influenced by the interplay between predator and prey strategies (Lima, 2002), and the combination of these probabilities ultimately determines the level of predation risk prey are exposed to (Lima and Dill, 1990). An influential approach to identifying the optimal foraging strategies adopted by predators is to establish which decisions maximise the net rate of energy gain, thereby maximising a crucial element of the predator’s fitness (Stephens and Krebs, 1986). As many predators are themselves killed by other predators (Sergio and Hiraldo, 2008; Lourenço *et al*., 2014), or face threats from dangerous prey (Mukherjee and Heithaus, 2013), predators also face selection to adopt strategies which balance energy gain with the need to minimise risk (Brown and Kotler, 2004). The response of an individual predator to this trade-off additionally depends on its state (Houston *et al*., 1993; Brown and Kotler, 2004; Berger-Tal and Kotler, 2010), which encompasses the range of internal attributes influencing the costs and benefits of pursuing a particular behavioural strategy (Houston and McNamara, 1999). Predators also adjust their hunting tactics in response to the behaviour of prey (Cresswell and Quinn, 2004; Cresswell and Quinn, 2010; Embar, Mukherjee and Kotler, 2014), and use information gathered during interactions with prey to negotiate a range of trade-offs encountered while hunting (Barnett *et al*., 2012; Embar *et al*., 2014; Smith *et al*., 2020a).

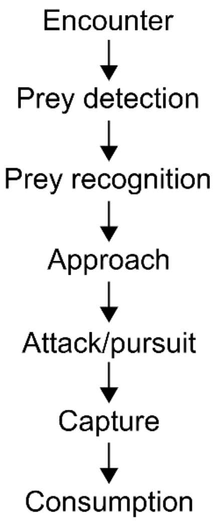

Figure 1.1: Steps in the sequence of events describing a predator-prey interaction, adapted from Lima and Dill (1990) and Kelley and Magurran (2011). Shown from the predator's perspective, the sequence starts with the initial encounter between the predator and the prey, which is defined as the moment when the predator moves within sufficiently close range that it can feasibly detect or be detected by prey (Lima and Dill, 1990). In the subsequent prey detection and recognition steps, the predator becomes aware of and appropriately categorises prey as a suitable target (Kelley and Magurran, 2011). In many predator-prey systems, these steps are followed by an approach phase, in which the predator slowly moves towards the prey, before initiating an attack or pursuit. The penultimate capture step is separated from prey consumption, as even at this late stage prey can deploy defences which disrupt the attempts of predators to subjugate and kill the prey (Recher and Recher, 1968; Whitford *et al*., 2019).

Despite research highlighting the sophistication of decision-making by foraging animals (Stephens, 2007), models exploring predator-prey population dynamics or the evolution of prey defences have historically relied on simplified versions of predator behaviour (Lima, 2002). Predator populations and the threat they pose to prey have typically been represented using static population averages (Pettorelli *et al*., 2011), limiting the ability of predators to respond flexibly to prey (Lima, 2002). While all models are abstractions of a complex reality, expectations about optimal prey defences can be altered radically when more realistic features of predator behaviour are accounted for in theoretical models, including the influence of the predator's condition or nutritional state on foraging decisions (Sherratt, 2003; Kokko, Mappes and Lindström, 2003; Aubier and Sherratt, 2020) and variation in the predator's hunting tactics (Jackson *et al*., 2006; Tosh, 2011; Morrell, Ruxton and James, 2011; Gal, Alpern and Casas, 2015; Morrell, Greenwood and Ruxton, 2015). Knowledge of predator cognition can also be instrumental in predicting patterns of selection by predators on prey traits (Bond, 2007; Mitchell, 2009; Aubier and Sherratt, 2015; Thorogood, Kokko and Mappes, 2018), demonstrating the value of understanding the constraints acting on predator behaviour. Finally, the use of population averages to represent the risk predators pose to their prey conflicts with growing evidence for variation in the behaviour of individual predators, or animal personality differences, which have the potential to influence how interactions between predators and prey advance from one stage to the next (Sih *et al*., 2012; Wolf and Weissing, 2012).

Personality variation is defined as consistent inter-individual differences in behaviour, which persist over time or remain correlated across contexts (Réale *et al*., 2007; Dall *et al*., 2012). For a given behavioural trait, differences of this kind account for approximately 35% of the total variance (Bell, Hankison and Laskowski, 2009), and have been shown to be heritable (Dochtermann, Schwab and Sih, 2015), with repercussions for fitness (Smith and Blumstein, 2008). Theoretical models suggest that personality variation can arise via a variety of mechanisms, including as a consequence of initial differences in an animal's state (Dingemanse and Wolf, 2010). Even for state variables which fluctuate dramatically over relatively short time-scales, positive feedbacks between state and behaviour can facilitate the emergence of stable inter-individual differences over time (Rands *et al*., 2003; Wolf *et al*., 2007; Luttbeg and Sih, 2010; Sih *et al*., 2015). One of several possible feedback mechanisms involves the conflict between investment in current reproduction over future reproductive attempts (Wolf *et al*., 2007). Given this trade-off, positive feedbacks can arise when the expected reproductive success of an individual in the future shapes current behaviour, such as the propensity to take risks (Clark, 1994; Nicolaus *et al*., 2012), which in turn is proposed to reinforce initial differences between individuals in the allocation of reproductive investment (Sih *et al*., 2015). Temporal variability in the selective environment may also promote the coexistence of different personality or behavioural types within natural populations, if individuals with contrasting personalities are adapted to different ecological conditions (La Cœur *et al*., 2015; Nicolaus *et al*., 2016). In other theoretical models, personality variation can also emerge when negative frequency-dependent selection, generating variation, is combined with social responsiveness, which promotes consistency (Dall, Houston and McNamara, 2004, Wolf, Van Doorn and Weissing, 2011; Johnstone and Manica, 2011).

Many of the studies exploring the impact of personality on predator-prey interactions have focused on prey activity and boldness, as both traits are connected with the trade-off between gathering resources and exposure to predation risk (Lima and Dill, 1990; Werner and Anholt, 1993; Anholt and Werner, 1995). Activity levels are often correlated with boldness (Pintor, Sih and Bauer, 2008; Wilson and Godin, 2009; Cote *et al*., 2010), which has been defined as the extent to which individuals place more weight on acquiring resources at the cost of reduced risk avoidance (Wilson *et al*., 1993; Ward *et al*., 2004; Réale *et al*., 2007), and is typically assessed by measuring how individuals respond to risky novel environments or potentially threatening stimuli (Carter *et al*., 2013). Bold animals are more tolerant of risky situations compared to shy individuals (Ward *et al*., 2004; Harcourt *et al*., 2009a), and are therefore more susceptible to predators (Bremner-Harrison, Prodohl and Elwood, 2004; Bell and Sih, 2007; Smith and Blumstein, 2008; Carter *et al*., 2010; Belgrad and Griffen, 2016; Hulthén *et al*., 2017; Ballew, Mittelbach and Scribner, 2017; Lapiedra *et al*., 2018; Balaban-Feld *et al*., 2019a), although bold individuals may be able to counterbalance their increased vulnerability to predators through improvements in their condition (Moiron, Laskowski and Niemelä, 2020). Bold individuals also resume foraging more rapidly in the aftermath of disturbance (van Oers *et al*., 2004), but are slower to respond to imminent danger than shy individuals (Quinn and Cresswell, 2005; Jones and Godin, 2010), suggesting that personality traits can affect levels of anti-predator vigilance (although see Couchoux and Cresswell, 2012). In natural populations experiencing significant predation pressure, boldness also tends to be correlated with inter-individual variation in exploratory behaviour and aggressiveness towards conspecifics, implying that survival in the face of a pervasive predation threat is facilitated by specific combinations of behavioural traits (Bell, 2005; Bell and Sih, 2007; Dingemanse *et al*., 2007; Dhellemmes *et al*., 2020).

While behavioural differences between individual predators are known to influence rates of prey consumption (Exnerová *et al*., 2010; Griffen, Toscano and Gatto, 2012; Pruitt, Stachowicz and Sih, 2012; Toscano and Griffen, 2014; Michalko and Řežucha, 2018), resolving the impact of predator personality on prey across diverse predator-prey systems is likely to require knowledge of how personality affects predator decision-making at multiple stages of the predation sequence (**Fig. 1.1**). Despite the accumulating evidence for links between personality variation, inter-individual differences in movement (Spiegel *et al*., 2017) and cognition (Sih and Del Giudice, 2012; Griffin, Guillette and Healy, 2015), the effects of personality variation on the cognitive processes involved in encountering, detecting and successfully capturing prey have not been comprehensively explored. In the introduction to this thesis, I provide an overview of the known and likely effects of personality variation on predator behaviour at different stages of the predation sequence (Section 1.2), before focusing on how personality may influence how predators alter their behaviour flexibly (Section 1.3). Since the impact of many predatory species on prey is also strongly linked to the behaviour of other predators, I also discuss how personality variation may shape interactions between predators of the same species (Section 1.4). I then briefly outline what is known about how predator personality relates to the extensive scientific literature on individual foraging specialisations (Section 1.5), before exploring the impact of predator personality on prey in more detail (Section 1.6). I conclude with an outline of the predator-prey systems studied in this thesis, and a brief description of the questions addressed in subsequent chapters (Section 1.7).

1.2 Impact of personality variation on predator behaviour at different stages of the predation sequence

1.2.1 Encounter rates with prey

Remote tracking of animal movements within wild populations has demonstrated that individuals differ markedly in their movement, habitat preferences and space use, including in traits such as distance travelled over a fixed time period, home range size and site fidelity (Kobler *et al*., 2009; Harrison *et al*., 2015; Nakayama, Rapp and Arlinghaus, 2016; Patrick and Weimerskirch, 2017; Villegas-Ríos *et al*., 2018; Hertel *et al*., 2019). In some instances, the magnitude of consistent inter-individual differences in movement traits can exceed the extent of variation between species (Harrison *et al*., 2019). Until recently, relatively few studies had integrated data on the movement patterns of animals in their natural environment with repeated behavioural tests under standardised conditions, but it is increasingly clear that inter-individual variation in space use is often correlated with traits such as activity or boldness (Boon, Réale and Boutin, 2008). Compared to their shy counterparts, bold sleepy lizards (*Tiliqua rugosa*) occupy larger home ranges (Spiegel *et al*., 2015), and in bank voles (*Myodes glareolus*), boldness is correlated with total movement distances (Schirmer *et al*., 2019). Consistent inter-individual differences in boldness are also associated with an individual's tendency to disperse more widely (Fraser *et al*., 2001; Cote *et al*., 2010), explore novel environments (Wilson and Godin, 2009; Quinn *et al*., 2012) and move continuously through their environment for longer periods without pausing (Wilson and Godin, 2010). Research on the relationship between personality variation and space use therefore suggests that more active or bolder predators are likely to move through their environment at a faster rate, increasing the probability of encountering prey (Ioannou, Payne and Krause, 2008).

Boldness is also expected to affect encounter rates with prey by influencing the total amount of time animals spend in dangerous habitats (Schirmer *et al*., 2019; Sommer and Schmitz, 2020) or actively searching for prey under risky conditions (Ioannou, Payne and Krause, 2008; Farwell and McLaughlin, 2009; Wilson *et al*., 2011; Balaban-Feld *et al*., 2019a). In support of this prediction, individual mud crabs (*Panopeus herbstii*) which spent more time outside of a safe refuge consumed more prey items than individuals exhibiting greater refuge use, but this effect was only apparent when crabs were exposed to cues indicating the presence of one of their own predators (Griffen, Toscano and Gatto, 2012). Similarly, the activity levels of individual jumping spiders (*Marpissa muscosa*) were positively correlated with the amount of time spent in a zone immediately surrounding a food source situated in a risky context, further substantiating the link between activity levels and the propensity of individuals to prioritise acquiring resources over safety (Steinhoff *et al*., 2020). Studies exploring the link between within-population variation in life history and behaviour provide further support for the effect of boldness on the time spent foraging under predation risk. Based on the pace-of-life-syndrome hypothesis, individuals with fast life histories characterised by rapid growth, high metabolic costs and increased investment in current reproduction are expected to sustain higher energetic requirements through increased activity and boldness (Wolf *et al*., 2007; Réale *et al*., 2010). This strategy helps maximise energy intake by increasing encounter rates with prey, but is predicted to come at the cost of future reproduction and longevity. Acoustic telemetry of wild Eurasian perch predators (*Perca fluviatilis*) has shown that individuals with a fast life history move through their environment at a higher rate and spend a greater amount of time foraging in risky habitats, compared to individuals with a slow life history (Nakayama, Rapp and Arlinghaus, 2016). However, while many studies report a correlation between life history, behaviour and physiology, others fail to find any such link (Royauté *et al*., 2018), possibly because the strength of the association between these traits may vary with ecological conditions including the level of predation risk predators are themselves exposed to (Mathot *et al*., 2015; Montiglio *et al*., 2018).

Consistent with the prediction that bold or more active predators encounter prey more frequently, an experiment in a controlled mesocosm setting demonstrated that prey survival is determined by the interplay between predator and prey behavioural types (Pruitt, Stachowicz and Sih, 2012). In this mesocosm study, relatively active ochre sea star (*Pisaster ochraceus*) predators were found to preferentially consume black turban snail (*Chlorostoma funebralis*) prey displaying less pronounced avoidance of predator cues, whereas relatively inactive predators were more likely to kill prey showing stronger avoidance behaviour. These results resemble the predictions of the locomotor crossover hypothesis, which predicts how differences in foraging mode between predator species influences rates of encounter with prey and ultimately dictates the composition of a predator's diet (Huey and Pianka, 1981). In this hypothesis, predators which actively search for prey are expected to disproportionately encounter and consume sedentary prey species, whereas predators adopting a sit-and-wait tactic are expected to encounter and consume wide-ranging, mobile prey. Whether these effects persist outside of a highly simplified mesocosm setting is an open question, given that predation risk can differ between habitats, and that prey with contrasting personalities are likely to differ in their use of safe areas (Sommer and Schmitz, 2020).

For predators which search for prey over large spatial scales, personality is also likely to influence encounter rates further by shaping the search strategies of individual predators. A study on Northern gannets (*Morus bassanus*) revealed inter-individual consistency in the response of birds to proxies for prey abundance and the use of foraging locations, suggesting that individual predators differ in how they adjust their search intensity in response to environmental gradients (Patrick *et al*., 2014). In wandering albatrosses (*Diomedea exulans*), boldness levels are also associated with the propensity of individuals to switch to novel foraging locations, rather than remaining within the same foraging patch (Patrick, Pinaud and Weimerskirch, 2017). Bold birds adopted a strategy which involved a greater number of visits to different foraging patches, but also less intensive foraging within patches, suggesting that bold individuals place greater weight on gathering information on prey through exploration of their environment. Studies which have measured the response of individuals to experimental manipulations in the distribution of food resources shed further light on how personality variation may be related to consistent inter-individual differences in the tendency to sample alternative foraging options within their environment (Krebs, Kacelnik and Taylor, 1978; Shettleworth *et al*., 1988). Following a sudden shift in the distribution of resources, individual great tits (*Parus major*) which showed an increased tendency to explore a novel environment under standardised conditions ('fast explorers') were found to switch to new foraging locations more rapidly than 'slow explorers' (van Overveld and Matthysen, 2010), and were also less likely to revisit depleted food patches (van Overveld and Matthysen, 2013; Arvidson and Matthysen, 2016). For predators which roam widely in search of patchily distributed prey, personality-related differences in search strategies may therefore reflect different approaches to obtaining information on the available foraging options (Mathot *et al*., 2012), and the balance between acquiring information on prey in newly visited areas versus continued exploitation of known resource patches (Kramer and Weary, 1991). Bold individuals or those showing a greater tendency to explore novel environments (fast-exploring individuals) are likely to prioritise sampling novel areas, enabling them to respond more quickly to a shift in resources, which is thought to be advantageous in environments with evenly distributed resources (Mathot *et al*., 2012). In contrast, slow exploring individuals with a greater tendency to engage in thorough and intensive area-restricted search are expected to forage more efficiently in environments where resources are clustered (Spiegel *et al*., 2017).

Personality variation may also be relevant to predators adopting sit-and-wait hunting tactics, which typically involve ambushing prey at sites where prey are abundant (Tutterow *et al*., 2020) or where prey are more vulnerable to being caught (Savino and Stein, 1989; Balme, Hunter and Slotow, 2007). Relatively little is known about whether individuals differ consistently in their ambush site selection, although one recent study has shown that the distance moved by individual antlion larvae (*Myrmeleon hyalinus*) between successively constructed ambush sites is repeatable across different micro-habitats (Alcalay, Scharf and Ovadia, 2014). Moreover, instead of following the same tactic in all circumstances, many predator species switch flexibly between active and sit-and-wait hunting modes (Huey and Pianka, 1981; Cresswell and Quinn, 2010; Higginson and Ruxton, 2015). Studies tracking animal movement patterns in the wild have also documented consistent differences in the tendency of individuals to remain in one location or actively patrol their environment in search of prey (Towner *et al*., 2016), or switch between inactive and active foraging modes (Nakayama, Rapp and Arlinghaus, 2016). There is also some evidence to suggest that personality may play a role in biasing the preference of individual predators for one hunting mode over another (Wilson and McLaughlin, 2007). Since actively searching for prey is likely to increase encounter rates with prey at the cost of increased exposure to other threats (Higginson and Ruxton, 2015), this strategy may be favoured by bold individuals which are typically relatively impervious to external threats such as predators.

1.2.2 Prey detection

By influencing how predators move through their environment, personality variation also has the potential to affect the probability that prey will be detected or recognised. Even if a predator has approached within close range of prey, camouflaged or motionless prey may still avoid detection (Ioannou and Krause, 2009). While the predator's overall search rate (i.e. the total area searched) is expected to be positively correlated with the rate at which prey are encountered, high search rates can limit the amount of time a predator can spend searching for prey within a subset of the area covered, and therefore come at the cost of a reduced probability of detecting prey (Gendron and Staddon, 1983; Gendron and Staddon, 1984). As individuals with a greater exploratory tendency tend to move between patches more rapidly but also search less intensively within a patch, predators with this behavioural type might be expected to detect prey at lower rates. Moreover, many animals, including predatory fish, cephalopods, lizards and birds, travel in discontinuous bursts, interspersed with pauses, in a form of movement known as 'intermittent locomotion' (Kramer and McLaughlin, 2001). Motion blur induced during periods of rapid forward movement could potentially interfere with visual perception, reducing the probability that stimuli are detected (Kramer and McLaughlin, 2001). Consistent with this hypothesis, predators have been observed to pause more frequently when searching for prey which are harder to detect (Avery *et al*., 1987; Ehlinger, 1989). Since bold individuals are known to spend longer in the rapid propulsive phase and pause for shorter periods of time (Wilson and Godin, 2010), consistent inter-individual differences in intermittent locomotion could further reinforce the likely effect of exploratory behaviour on prey detection. By contrast, as well as shaping the balance between forward movement and pauses, personality differences could also conceivably influence the range of viewing conditions a predator experiences as it moves through its environment. Specifically, if predators move through their environment at a higher rate, they are likely to view prey from a broader range of directions. As there is some evidence that the orientation of prey relative to an observer affects the probability that counter-shaded prey will be detected (Penacchio, Harris and Lovell, 2017), exposure to a variety of viewing angles might be particularly useful for predators attempting to locate cryptic prey in cluttered environments (Galloway *et al*., 2020). By enabling predators to view prey from a range of angles, exploration might have a beneficial effect on prey detection rates, opposing the expected impact of the link between exploration and the overall search rate.

In complex natural environments replete with a myriad of visual features, including varying colours, shapes, patterns and textures, the intensive visual search involved in detecting cryptic prey can be particularly challenging for predators. Many camouflage strategies operate by minimising the signal-to-noise ratio of the prey relative to the background (Merilaita, Scott-Samuel and Cuthill, 2017), but one way in which predators can counteract this defensive tactic is to form search images for specific prey types (Langley *et al*. 1996; Bond and Kamil 1999). Search images represent the enhanced prey detection or recognition gained through increasing experience with a specific prey type, and involve predators focusing their attention on salient features of their target (Bond and Kamil, 2002). Due to inherent limits on the rate at which animals can process information (Dukas, 2002), focusing attention on specific prey types can restrict how much attention can be devoted to other activities such as anti-predator vigilance, and can therefore reduce animals' ability to detect peripheral stimuli which might represent a threat (Dukas and Kamil, 2000). If animals show a decline in anti-predator vigilance over the course of a search, this effect could potentially offset the predicted negative relationship between search rate and the probability of prey detection (Ioannou, Ruxton and Krause, 2008). Since the bold-shy continuum reflects an individual's tendency to prioritise gaining access to food at the expense of their own safety, bolder predators might be expected to relax their anti-predator vigilance more quickly, and focus their attention on searching for prey.

1.2.3 Predator approach and attack behaviour

Once a predator has detected its prey, it faces a series of decisions about whether and when to approach or initiate an attack. Several studies have demonstrated that individual predators vary consistently in the time taken to approach or attack prey following an encounter and have shown that these differences are correlated with personality traits. For example, funnel-web spiders (*Agelenopsis aperta*) displaying greater aggressiveness towards conspecifics were also quicker to attack prey, and emerged more rapidly from a refuge following a simulated attack from a potential predator (Riechert and Hedrick, 1993). Research on predatory invertebrates has additionally demonstrated that inter-individual differences in the latency to attack prey, or the number of attempts required to capture prey, are correlated with inter-individual variation in activity levels (Blackenhorn and Perner, 1994; Kralj-Fišer and Schneider, 2012) or aggressiveness towards conspecifics (Pruitt, Riechert and Jones, 2008; Foellmer and Khadka, 2013; Chang *et al*., 2017). Fast-exploring great tits (*Parus major*) also show less initial wariness when attacking unfamiliar aposematic prey compared to slow-exploring individuals, suggesting that the effectiveness of warning colouration is dependent on the predator's behavioural type (Exnerová *et al*., 2010). However, none of these studies was able to isolate the potential impact of personality variation on prey detection from its possible effects on the time taken to attack after the prey has been detected.

Multiple studies have also quantified inter-individual variation in the response of predators to prey, without examining whether differences between individuals are correlated with typically studied personality traits. For example, individual antlion (*Myrmeleon hyalinus*) larvae differ consistently in their latency to respond to prey (Alcalay, Scharf and Ovadia, 2015). During unconstrained interactions with single three-spined stickleback (*Gasterosteus aculeatus*) prey in a laboratory setting, individual pike (*Esox lucius*) predators were found to differ consistently in the time to taken to orient towards and attack sticklebacks, ultimately influencing the time taken to capture their target (McGhee, Pintor and Bell, 2013). Under natural conditions, the use of miniaturised time-depth recorders has also revealed inter-individual variation in the behaviour of wild seabirds, which may in part reflect differences in prey approach or pursuit behaviour, such as the duration, depth and shape of foraging dives (Woo *et al*., 2008; Potier *et al*., 2015), although these differences are also likely to reflect specialisation on different prey types (Elliot *et al*., 2008; see Section 1.5).

Predators tend to be slower to attack when prey deploy defences which overwhelm the predator's limited information-processing capacity, such as aggregation at high densities or coordinated motion within a group (Ioannou *et al*., 2009; Ioannou, Guttal and Couzin, 2012). By absorbing much of a predator's limited information-processing capacity, attempts to overcome the confusion effect by targeting prey within a dense group can come at the cost of a reduced ability to detect imminent danger (Milinski, 1984). In this situation, the important goal of making a rapid decision conflicts with the need to invest time in overcoming prey defences, generating a trade-off between decision speed and the ability of the predator to accurately target prey. Trade-offs between speed and accuracy might be relevant to multiple aspects of predator behaviour (Chittka, Skorupski and Raine, 2009), including to the ability to distinguish between defended and undefended prey types, which can be cognitively demanding when prey are encountered sequentially (Beatty and Franks, 2012). Intriguingly, there is evidence that some individuals consistently make fast but inaccurate decisions, whereas others make slow but accurate choices (Moiron, Mathot and Dingemanse, 2016). For example, individual archerfish (*Toxotes chatareus*) which took longer to shoot jets of water at targets were more accurate than rapidly shooting individuals in a colour discrimination task, but this trade-off only emerged when the task was sufficiently demanding (Jones *et al*., 2020). Bold individuals might be expected to forgo their own safety and make rapid decisions at the expense of accuracy (Sih and Del Giudice, 2012), raising the prospect that personality differences influence further aspects of predator decision making. Although there is currently mixed support for this prediction (Mamuneas *et al*., 2015; Mazza *et al*., 2019), the implications of personality-related speed-accuracy trade-offs for predator-prey interactions are only starting to be explored (Chang, Ng and Li, 2017).

1.3 The relationship between personality variation and behavioural plasticity and its consequences for predator behaviour

Predators must also confront the challenges imposed by a changing environment, including the need to track shifting prey distributions and overcome variable prey defences. Although personality differences are defined as consistency in individual behaviour over time and across different environmental contexts (Réale *et al*., 2007), on average only 35% of behavioural variation can be attributed to inter-individual differences (Bell, Hankison and Sih, 2009). Therefore, while the existence of animal personality necessarily implies that there are limits on the extent to which individuals can change their behaviour in different situations, or behavioural plasticity, there is still considerable space for individuals to adjust their behaviour to changing environmental circumstances (Dingemanse and Wolf, 2013). While some studies indicate that all individuals modify their behaviour across different contexts to the same extent (Houslay *et al*., 2018), others suggest that the degree of behavioural plasticity shown by an individual may be personality-dependent (Koolhaas *et al*., 2010; Stamps, 2016). It has been suggested that bold individuals are more likely to rely on their previous experiences, and exhibit reduced plasticity compared to shy individuals, which are predicted to sample more exhaustively and therefore be more sensitive to changes in their environment (Coppens, de Boer and Koolhaas, 2010; Mathot *et al*., 2012). Empirical tests of these predictions take two forms. Firstly, a number of studies have examined how average levels of boldness (or some other personality trait) are correlated with the level of plasticity in the same behaviour. The majority of these studies show that bold individuals tend to exhibit less plasticity in their risk-taking behaviour over time (Dammhahn and Almeling, 2012; Jolles *et al*., 2019), across environments (Kareklas *et al*., 2016) and in different social contexts (Magnhagen and Bunnefeld, 2009; Ólafsdóttir and Magellan, 2016), although there are exceptions to this general trend (Dingemanse *et al*., 2011; Kim, 2016). Secondly, other studies have tested whether personality variation is correlated with the degree of plasticity shown in other unconnected behavioural traits, and have generally shown that bold individuals are less responsive to a change in predation risk (Jones and Godin, 2010), resource availability (Spiegel *et al*., 2015) or temperature (Villegas-Ríos *et al*., 2017). In another study, shy kittiwakes (*Rissa tridactyla*) were shown to be less site-faithful during foraging trips compared to bold birds, which is consistent with the hypothesis that individuals with contrasting personalities vary in their use of environmental cues when searching for prey (Harris *et al*., 2019). Given these findings, the effect of personality on the degree of behavioural plasticity shown by predators may therefore complicate expectations based on the straightforward impact of personality on encounter rates with prey.

Personality variation also has the potential to influence the flexibility of predator behaviour through its effect on learning. While our understanding of the role of learning in predator behaviour is far from complete (Kelley and Magurran, 2011), learning is likely to play a vital role in enabling predators to switch between prey types (Croy and Hughes, 1991; Page and Ryan, 2005), track shifts in resource quality or prey populations (Krebs and Inman, 1992; Sims *et al*., 2006) and develop habitat- or prey-specific hunting techniques (Chen *et al*., 1996; Reid, Seebacher and Ward, 2010). Bluegill sunfish (*Lepomis macrochirus*) learn to adjust their prey search tactics to meet the challenges posed by foraging in different habitats (Ehlinger, 1989), but the existence of distinct behavioural types in this species generally limits the capacity of individuals to adjust their behaviour with increasing experience (Ehlinger and Wilson, 1988). Sih and Del Giudice (2012) have also suggested that the bold-shy behavioural axis may be correlated with an individual’s cognitive style, which they define as the way in which individuals gather, process and use information. Whereas bold individuals are expected to learn associations more quickly, based on their tendency to encounter novel stimuli at a higher rate (Dugatkin and Alfieri, 2003; Guillette *et al*., 2009; Trompf and Brown, 2014), individuals with this behavioural type are expected to be less adept at reversing previously learned associations following a change in the environment (Verbeek, Drent and Wiepkema, 1994). Intriguingly, in one study, individual pike which were able to reverse a learned association more rapidly took longer to capture prey in a live predation trial (Pintor *et al*., 2014), implying that there may be a trade-off between the ability to efficiently target specific prey types and flexibility in foraging behaviour. More broadly, while Sih and Del Giudice's predictions have been confirmed in some empirical studies (Guillette *et al*., 2009; Guillette *et al*., 2011; Bensky and Bell, 2020), a recent meta-analysis concluded that the direction of the relationships between personality traits and learning are highly variable (Dougherty and Guillette, 2018). The absence of consistent trends reflects the likely reality that any connections between personality and cognitive traits will depend on nature of the association to be learned (Griffin, Guillette and Healy, 2015). For example, great tits with reduced exploratory tendencies learn to avoid aposematic prey more quickly than fast-exploring individuals (Exnerová *et al*., 2010), in sharp contrast to the expectation that high levels of exploration promote rapid initial learning. Relatively risk-averse, shy predators may therefore be more adept at forming associations between cues and aversive stimuli, such as chemically defended prey, whereas bold predators may be quicker to learn in contexts where excessive caution is a hindrance to the acquisition of novel foraging skills (Sih and Del Giudice, 2012).

1.4 Predator personality and the social context

Social interactions between predators can have a range of consequences for prey, extending from reductions in the risk prey experience as a result of competitive interactions between otherwise solitary conspecifics (Peckarsky and Cowan, 1991; Clark *et al*., 1999) to the enhanced prey capture success experienced by predators living in groups (Lang and Farine, 2017). Personality variation can potentially shape these effects by influencing how individual predators interact with one another. In situations where prey are scarce, asymmetries in the ability of individual predators to monopolise limited or concentrated resources can have an important impact on hunting strategies (Gende and Quinn, 2004; López-Bao *et al.*, 2011). Even though the level of aggression expressed by an individual during a contest is expected to be dependent on the identity of its opponent (Briffa, Sneddon and Wilson, 2015), there is some indication that individuals differ consistently in aggressiveness (Wilson, Grimmer and Rosenthal, 2013). The competitive ability or social dominance of bold individuals is also typically greater than shy individuals (Webster, Ward and Hart, 2009; David, Auclair and Cézilly, 2011; Cole and Quinn, 2012; Favati, Leimar and Løvlie, 2014). Studies in central place foragers highlight how the association between boldness and competitive ability can potentially shape the spatial distribution of predators. In both black-browed albatrosses (*Thalassarche melanophris*) and Cory's shearwaters (*Calonectris borealis*), bold individuals were found to search for prey in areas closer to the colony, where competition is expected to be amplified (Patrick and Weimerskirch, 2014; Krüger *et al.*, 2019).

The presence of nearby conspecifics can also drive improvements in foraging efficiency without requiring active cooperation between predators (Pitcher, Magurran and Winfield, 1982). Specifically, foraging animals often produce inadvertent cues which can be exploited by conspecifics to identify areas of high prey density (Clark, 2007; Weimerskirch *et al.*, 2010; Page and Bernal, 2019), inform decisions about whether to attack novel prey items (Hämäläinen *et al.*, 2020) or acquire novel hunting techniques (Tinker, Mangel and Estes, 2009; Allen *et al.*, 2013). The transmission of social information between predators can have important consequences for the spatial distributions prey should adopt to minimise encounter rates (Hamblin *et al.*, 2010), as well as the evolution of prey traits such as warning colours, which rely on predators being informed about the unpalatability of brightly coloured prey (Thorogood, Kokko and Mappes, 2018). Intriguingly, there is some evidence that individuals differ in their use of socially acquired information, with shy or slow-exploring individuals being more likely to act on social information (Kurvers *et al.*, 2010a; Smit and van Oers, 2019; although see Trompf and Brown, 2014). In species which form loose foraging groups, shy or slow-exploring individuals also tend to be more attracted to conspecifics, locate themselves at the centre of the group and maintain social associations which persist over time (Aplin *et al*., 2013; Aplin *et al*. 2014; Nakayama *et al*., 2016), raising the prospect that individuals differ in their social foraging strategies (Bergmüller and Taborsky, 2010). Within stable groups, individuals also exhibit consistency in their tendency to search for novel resources (the producer tactic) or exploit the efforts of other foragers (the scrounger tactic), suggesting that the theoretically predicted equilibrium frequencies of different foraging tactics may be attained through individual specialisation (Beauchamp, 2001; Morand-Ferron, Yu and Giraldeau, 2011). Given that bold individuals tend to roam more widely, these individuals might be expected to come into contact with novel foraging opportunities more rapidly and therefore adopt the producer tactic more often (Dubois, Giraldeau and Réale, 2012), although empirical evidence for this relationship is mixed (Kurvers *et al*., 2010b; Jolles, Ostojić and Clayton, 2013; Aplin and Morand-Ferron, 2017). Finally, the extent to which personality differences are expressed in a social context is likely to depend on whether feedbacks between interacting individuals reinforce or counteract inter-individual variation (Webster and Ward, 2011; McDonald *et al*., 2016).

1.5 Individual specialisation and its links to predator personality

Alongside the extensive literature on animal personality, a related body of research has documented widespread and substantial evidence for individual foraging specialisations in wild predator populations, which cannot be explained by variables such as sex, age or morph type (Bolnick *et al*., 2003). Rather than being composed of generalist individuals with a broad dietary niche encompassing the entire range of prey types consumed by the predator population, many natural populations consist of individuals which specialise on a limited subset of the population’s overall resource base (Araújo, Bolnick and Layman, 2011). Empirical evidence suggests that niche differentiation within predator populations is driven by increasing levels of intra-specific competition for limited resources (Svanbäck and Bolnick, 2007; Kernaléguen *et al*., 2015; Sheppard *et al*., 2018), as well as release from competition with other species (Knudsen *et al*., 2007). Low overall prey abundance (Tinker, Bentall and Estes, 2008; Robertson *et al*., 2015), the existence of a diverse range of alternative prey types (Darimont, Paquet and Reimchen, 2009) and higher levels of predictability in the spatial distribution of prey (Courbin *et al*., 2018) also promote individual specialisation.

Despite the close association between individual specialisation in diet and the use of distinct foraging strategies or behaviours (Estes *et al*., 2003; Tinker *et al*., 2007; Woo *et al*., 2008; Baylis *et al*., 2015), it is unknown whether widely studied personality traits (as measured in standardised tests) predict specialisation in diet in the wild (Toscano *et al*., 2016). It is also unclear whether consistent inter-individual differences in foraging behaviour are a cause or a consequence of preferences for particular prey types, or whether the reported association between the two is underpinned by other factors linked to life history strategies. Analysis of stable isotope ratios in wild burbot (*Lota lota*) has revealed that monthly movement rates are positively correlated with increased consumption of relatively mobile pelagic prey, but only among more piscivorous individuals (Harrison *et al*., 2017). While these relationships could be explained if activity levels determine prey preferences, the same trend could also emerge if the choice of prey drives individual movement patterns. There is some evidence for the latter possibility in red knot (*Calidris canutus*), in which preferences for different prey types are responsible for generating variation in the size of digestive organs (gizzard mass), which in turn shape consistent inter-individual differences in behaviour (Oudman *et al*., 2016). More research combining standardised measures of personality, observations of predatory behaviour and indices of trophic niche width is therefore needed to fully resolve the complex links between the behaviour and prey choice of individual predators.

1.6 Consequences of predator personality variation for prey

While the specific ways in which personality influences predatory behaviour are still somewhat unclear, there is evidence to suggest that predator personality has meaningful impacts on prey. Laboratory and mesocosm studies of predator-prey interactions have demonstrated that the survival probability of prey is influenced by the predator's personality, suggesting that the behavioural type of the predator could be an important factor influencing the strength of selection on prey traits in the wild (Exnerová *et al*., 2010; Nyqvist *et al*., 2012; Smith and Blumstein, 2010; McGhee, Pintor and Bell, 2013; Start and Gilbert, 2017; Michalko and Řežucha, 2018). Further mesocosm studies also indicate that predation risk depends on an interaction between the personality type of both the predator and the prey (Pruitt, Stachowicz and Sih, 2012; Chang *et al*., 2017). If this pattern holds in natural environments, these results imply that the selective pressures which prey must contend with depend on frequency of the predator type which poses the greatest threat, given the prey's own personality (Sih *et al*., 2012; McGhee, Pintor and Bell, 2013). This potentially creates the conditions for variation in predator and prey behavioural traits to be maintained through cyclical changes in the strength of reciprocal frequency-dependent selection (Sinervo and Calsbeek, 2006; Pruitt, Stachowicz and Sih, 2012).

Predators can also significantly influence prey via non-consumptive or non-lethal effects, which occur when increased levels of predation risk trigger an elevated anti-predator response or heightened physiological stress in prey, resulting in negative effects on prey growth, survival or reproduction (Lima and Dill, 1990; Lima, 1998; Clinchy, Sheriff and Zanette, 2013; Sheriff *et al*., 2020). The non-consumptive impacts of predators are likely to be pervasive (Peckarsky *et al*., 2008), and the magnitude of these effects on prey demography and ecosystem-level processes can sometimes surpass those of direct prey consumption (Preisser, Bolnick and Benard, 2005; Schmitz, Hawlena and Trussell, 2010). Even though the potency of non-consumptive effects is likely to be influenced by the attributes of the predator, including its hunting mode (the predator's position along the continuum between active and sit-and-wait/ambush tactics), habitat domain (the spatial area over which predators typically hunt) and motivational state (Wirsing *et al*., 2020), the possibility that the strength of non-consumptive effects could vary with predator personality has received little attention. Although one study has reported that foraging by palmate newts (*Lissotriton helveticus*) is suppressed to a greater extent in the presence of aggressive goldfish (*Carassius auratus*), relative to less aggressive fish (Winandy and Denoël, 2015), it was not evident in this study whether the goldfish were acting as predators or competitors. Whether predator personality shapes prey anti-predator responses therefore remains unclear. Predators with an active foraging mode, which hunt over a large area, also tend to produce relatively weak non-consumptive effects compared to predators using sedentary sit-and-wait tactics (Preisser, Orrock and Schmitz, 2017; Miller, Ament and Schmitz, 2014; Murie and Boardeau, 2019), potentially because cues from predators following different hunting strategies vary in how accurately they predict levels of predation risk within a specific location (Luttbeg and Trussell, 2013). Since personality variation strongly influences predator movement traits, personality traits such as boldness might have a similar impact on the strength of non-consumptive effects.

Through their consumptive and non-consumptive impact on prey populations, predators can also indirectly influence the abundance and community composition of consumers at lower trophic levels, which in turn can ultimately have repercussions for processes operating at the scale of entire ecosystems (Peckarsky *et al*., 2008; Schmitz, Hawlena and Trussell, 2010; Burkholder *et al*., 2013). Intra-specific variation in the traits of predators which influence interactions with prey, such as body size and morphology, are known to be important determinants of the impact of predators on prey communities (Bolnick *et al*., 2011; Pettorelli *et al*., 2011). A recent meta-analysis found that the effects of intra-specific variation are strongest and can outweigh species-level differences when interactions between species occur indirectly, as would be the case in a trophic cascade, in which the impact of predators on their prey has further ramifications for the abundance of organisms at lower trophic levels (Des Roches *et al*., 2018). Given that consistent differences in the behaviour of individual predators can strongly influence interactions with prey (Pruitt, Stachowicz and Sih, 2012; McGhee, Pintor and Bell, 2013), predator personality variation might also be expected to modulate the strength of predator effects on prey communities (Bolnick *et al*., 2011). The results of research on predator-prey interactions in closely controlled mesocosms provide a simple demonstration of these effects (Royauté and Pruitt, 2015; Start and Gilbert, 2017; although see Ingram and Burns, 2018). Although it may be questionable whether conclusions drawn from mesocosm studies can be applied to more complex ecosystems, the observed effects of predator activity levels on the magnitude of trophic cascades (Start and Gilbert, 2017) are reminiscent of the impact of variation in the foraging-related morphological traits of predators on prey communities (Post *et al*., 2008).

More broadly, predator personality variation has the potential to affect the dynamics of prey communities through at least two general mechanisms. Firstly, if predator personality variation leads to inter-individual differences in prey attack rates, the existence of stable variation around the population mean can drastically alter model predictions concerning whether predator and prey populations should fluctuate together or remain stable over time (Okuyama, 2008; Bolnick *et al*., 2011). This effect arises because of Jensen's inequality, which applies when the functional response (describing how prey consumption changes with prey density, attack rate and handling time) is non-linear, as is the case in many predator-prey systems (Jeschke, Kopp and Tollrian, 2002). Given variation in attack rates, Jensen's inequality implies that the rate of prey consumption obtained by evaluating the functional response at the population mean attack rate will over-estimate the mean rate of prey consumption which is actually achieved within the population. The size of this discrepancy depends on the extent of inter-individual variation in attack rates. When accounted for in models, variation in predator behaviour can reduce the amplitude of predator-prey population cycles, suggesting that it can be misleading to rely solely on population averages when attempting to model predator-prey dynamics (Okuyama, 2008). Secondly, within the network of predator-prey relationships comprising an ecosystem-scale food web, predators with contrasting personalities might vary in the number of other species they interact with (Bolnick *et al*., 2011; Moran, Wong and

Thompson, 2017). Differences in encounter and attack rates between individual predators could potentially magnify variation in the range of prey types consumed, increasing the capacity of food webs to withstand environmental change or to remain intact following the loss of constituent species (Moya-Laraño, 2011; Montoya, Pimm and Sole, 2006; O'Gorman and Emmerson, 2009). Personality variation could also influence the number of food web links between predators and other species if it affects the probability of intra-guild predation, as suggested by a recent study on predatory spiders (Michalko and Pekar, 2017). An increase in the frequency of individual predators displaying a tendency to target other species at the same trophic level could potentially further enhance food web stability and reduce the strength of trophic cascades (Finke and Denno, 2005).

1.7 Thesis overview: studying the effects of personality and cognition in predatory fish

The study of predator-prey interactions in freshwater aquatic ecosystems has yielded numerous insights, ranging from experimental confirmation that top predators cause cascading impacts on primary producers (Carpenter *et al*., 1987; Carpenter and Kitchell, 1988), to an understanding of how predation rates are influenced by environmental variables (Savino and Stein, 1982; Werner *et al*., 1983; Turesson and Brönmark, 2007). Detailed behavioural observations of interactions between predatory fish and shoaling prey have also helped to shape our understanding of predator hunting tactics and prey counter-strategies (Neill and Cullen, 1974; Magurran and Pitcher, 1987; Krause and Ruxton, 2002). When combined with extensive pre-existing knowledge of predator-prey ecology in freshwater aquatic environments, the widespread existence of habitat and diet specialisations within predatory fish populations (Werner *et al*., 1983; Svanbäck and Bolnick, 2007; Kobler *et al*., 2009; Nakayama, Rapp and Arlinghaus, 2016; Harrison *et al*., 2017) makes predatory fish an attractive system in which to study the consequences of personality variation.

Predatory fish have also been used as a model for understanding how predators adjust their foraging strategies flexibly. This body of research includes studies examining how predatory fish modulate their behaviour in response to changes in prey abundance (Murdoch, Avery and Smyth, 1975; Hughes and Croy, 1993), the challenges posed by hunting in particular habitats (Ehlinger and Wilson, 1988) and variation in prey traits (Milinski, 1979; Landeau and Terborgh, 1986; Krause and Godin, 1996; Ioannou *et al*., 2012; Penry-Williams, Ioannou and Taylor, 2018; Ioannou *et al*., 2019). While the ability of predators to adjust their behaviour appears to be in conflict with the notion of stable behavioural types, in fact, animal personality reflects the tendency of individuals to be biased towards one end of a continuous behavioural spectrum (Wilson *et al*., 1993), leaving considerable space for plasticity (Bell, Hankison and Laskowski, 2009). Both concepts serve to undermine the idea that predators pose a fixed and invariant risk to prey, first by highlighting how individual predators vary repeatably in the threat they pose, and second, by stressing that predators can dynamically respond to prey (Lima, 2002). In this thesis, I aim to explore how aspects of predator personality and cognition influence the risk prey experience by focusing on three species of fish: three-spined sticklebacks (*Gasterosteus aculeatus*), pike cichlids (*Crenicichla frenata*) and blue acara cichlids (*Aequidens pulcher*). These research questions include whether boldness predicts individual variation in the capacity of predators to detect cryptic prey (Chapter 2), how individual predators differ in their response to prey under natural conditions (Chapter 3), whether prey adjust their anti-predator behaviour when exposed to predators with contrasting personalities (Chapter 4) and whether unpredictable escape trajectories disrupt the ability of predators to improve their performance via learning (Chapter 5).

1.7.1 Three-spined sticklebacks

Three-spined sticklebacks (*Gasterosteus aculeatus*) are found in a wide variety of freshwater and coastal marine environments across the Northern hemisphere, having repeatedly colonised freshwater habitats following the last period of extensive glaciation (Bell and Foster, 1994). In freshwater, three-spined sticklebacks predominantly consume micro-crustacean prey including copepods, ostracods and cladocerans (e.g. *Daphnia magna*), as well as chironomid (midge) larvae and ephemopteran (mayfly) nymphs (Hynes, 1950). Although they are generally characterised as visual predators, olfaction is also important in alerting three-spined sticklebacks to the presence of prey in their immediate vicinity (Beukema, 1968; Webster *et al*., 2007; Johannesen, Dunn and Morrell, 2012). Laboratory experiments examining the response of three-spined sticklebacks to swarms of *Daphnia magna* prey have also highlighted the influence of hunger and perceived predation risk on predatory decision-making. Experiments using this system have shown that hungry sticklebacks are able to overcome the confusion effect by directing attacks towards dense regions of a *Daphnia* swarm (Heller and Milinski, 1979), but following a simulated predator attack, sticklebacks preferentially attack the edge of the prey group (Milinski and Heller, 1978). This switch in preferences is explained by the observation that the sticklebacks which direct attacks towards dense regions of the swarm are less able to detect a simulated predator attack (Milinski, 1984).

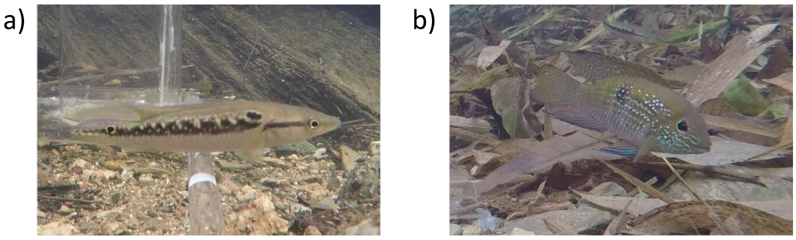

Figure 1.2: Photographs of the predatory fish species studied in this thesis: (a) pike cichlids (*Crenicichla frenata*) and (b) blue acara cichlids (*Aequidens pulcher*). Images are not scaled to reflect differences in body size.

Photographs in (a) and (b) are by A. W. Szopa-Comley.

The conflict between exposure to risk and resource acquisition also underpins correlations between boldness, activity, exploration and aggressiveness in three-spined sticklebacks (Huntingford 1976; Bell, 2005; Bell and Sih, 2007; Dingemanse *et al*., 2007). Correlations between these behavioural traits are tighter in populations exposed to higher levels of predation risk through the continuous presence of piscivorous birds and fish, compared with predator-free populations (Giles and

Huntingford, 1984; Bell, 2005; Bell and Sih, 2007; Dingemanse *et al*., 2007). Although bold three-spined sticklebacks are at greater risk of predation (Bell and Sih, 2007), these individuals also tend to emerge from refuges more rapidly following disturbance, exhibit higher rates of food intake, make quicker decisions and are more likely to adopt risky positions within groups than shy individuals (Ward *et al*., 2004; Ioannou, Payne and Krause, 2008; Webster, Ward and Hart, 2009; Harcourt *et al*., 2009a; Mamuneas *et al*., 2015; McDonald *et al*., 2016; Nakayama *et al*., 2016). Given the relevance of the bold-shy behavioural axis to multiple aspects of three-spined stickleback ecology, this species represents an interesting system in which to explore the connections between personality differences and predator behaviour. Accordingly, in Chapter 2, I begin this thesis by experimentally testing whether inter-individual variation in the response of three-spined sticklebacks to cryptic and conspicuous prey items is explained by boldness.

1.7.2 Pike cichlids and Trinidadian guppies

Over decades of research, evolutionary ecologists have documented pronounced differences in the colouration, life history and anti-predator behaviour of Trinidadian guppies (*Poecilia reticulata*) originating from two distinct environments within the rivers and streams of Northern Trinidad: downstream high-predation habitats supporting a relatively diverse assemblage of piscivorous fish, and upstream low-predation habitats which are devoid of any major predators (Seghers, 1974; Endler, 1980; Reznick and Endler, 1982; Magurran and Seghers, 1991). The divide between upstream high- and downstream low-predation environments is replicated in multiple watersheds across the rugged terrain of Trinidad’s Northern Range, and arises due to the presence of waterfalls, which prevent upstream dispersal of predatory fish including pike cichlids (*Crenichla frenata*, **Fig. 1.2a**). Pike cichlids are major predators of the guppy in high-predation habitats, and are therefore a key component of the community of predators producing the contrast between high- and low-predation guppy populations (Reznick, Bryga and Endler, 1990; Magurran, 2005). Predation by pike cichlids has also been established as the selective force driving the evolution of inconspicuous colouration in male guppies (Endler, 1980).

Observations of pike cichlids and a closely related species, *Crenicichla saxatilis*, indicate that these predators typically orient towards their target, before approaching within close proximity and eventually launching a strike at the prey’s centre of mass (Johansson, Turesson and Persson, 2004; Walker *et al*., 2005). High-speed videography of interactions between pike cichlids and guppies under controlled conditions shows that pike cichlids attack ballistically, meaning that the predator is largely unable to adjust its trajectory during the short phase of rapid acceleration which constitutes the strike (Heathcote *et al*., 2020). The probability of a successful escape by the prey critically depends on the ability of guppies to execute a fast-start evasion response speedily, with sufficient tangential acceleration to exit the strike path of the attacking predator, as well as other factors such as the speed and strike distance of the pike cichlid (Walker *et al*., 2005). Even during successful escapes, guppies routinely come within one body length of the pike cichlid’s mouth (Heathcote *et al*., 2020), emphasising the precarious balance between survival and death during an interaction.

While interactions between pike cichlids and guppies have not been studied in as much detail in the wild, experiments in artificial pools have shown that pike cichlids trigger a pronounced anti-predator response in groups of high-predation guppies, including enhanced shoaling and increased levels of predator inspection (Botham *et al*., 2006; Botham *et al*., 2008). During the dry season, both pike cichlids and guppies are also frequently confined to relatively isolated river pools which contain a limited number of individual predators (Magurran, 2005). This feature of the pike cichlid-guppy system makes it likely that guppies will be in frequent visual contact with the same individual predators over an extended period. On a practical level it also makes it feasible to repeatedly quantify the behaviour of the same individual fish under natural conditions. When combined with extensive pre-existing knowledge of guppy anti-predator behaviour, these attributes make the pike cichlid-guppy system a suitable model in which to investigate the effects of predator personality variation on prey. My research on the pike cichlid-guppy system includes both observations of predator behaviour in the wild and in a semi-controlled setting. In Chapter 3, I begin by quantifying how individual predators vary in their response to prey under natural conditions. In Chapter 4, using artificial experimental pools, I then investigate whether guppies adjust their anti-predator behaviour in response to the behaviour of individual pike cichlids, with the aim of exploring how predator personality affects the level of risk perceived by prey.

1.7.3 Blue acara cichlids

Compared to pike cichlids, blue acara cichlids (*Aequidens pulcher*, **Fig. 1.2b**) pose a less significant threat to Trinidadian guppies in the wild (Botham *et al*., 2006). Nevertheless, laboratory observations of interactions between blue acaras and guppies indicate that blue acaras are highly sensitive to aspects of prey behaviour when deciding whether to attack, such as the tendency of the prey to engage in predator inspection behaviour and the prey's vigilance state (Godin and Davis, 1995; Krause and Godin, 1996). When considered alongside field observations suggesting that blue acaras typically forage more actively than specialist ambush predators (Botham *et al*., 2005), these results suggest that blue acaras may hunt by opportunistically pursuing unwary prey. These aspects of blue acara biology make it an intriguing predator against which to test the effectiveness of prey anti-predator strategies, including those which are thought to exploit features of predator cognition, such as behavioural unpredictability in prey (Humphries and Driver, 1970). In the final experimental chapter of this thesis, Chapter 5, I therefore test how unpredictable prey escape trajectories affect predator behaviour, by developing an experimental system involving artificial robot-controlled prey and real blue acara predators. Finally in Chapter 6, by bringing together insights from Chapters 2-5, I discuss how considering the impacts of personality and cognition on predator decision-making might improve our overall understanding of predator-prey interactions, and highlight future avenues for research at the intersection of these two areas.

Chapter 2:

Predator personality and prey detection: inter-individual variation in responses to cryptic and conspicuous prey

An adapted version of this chapter has been published in the journal *Behavioral Ecology and Sociobiology*:

Szopa-Comley, A. W., Donald, W. G. and Ioannou, C. C. (2020) ‘Predator personality and prey detection: inter-individual variation in responses to cryptic and conspicuous prey’, *Behavioral Ecology and Sociobiology*, 74, 70. doi: https://doi.org/10.1007/s00265-020-02854-9

I led the writing of the paper, conducted experimental trials, analysed videos and undertook the statistical analyses, in discussion with my supervisor Christos C. Ioannou. William G. Donald conducted experimental trials and analysed videos, as part of his undergraduate research project at the University of Bristol.

2.1 Abstract

Limited attention constrains predators from engaging in cognitively demanding tasks such as searching for cryptic prey at the same time as remaining vigilant towards threats. Since finite attention can result in negative correlations between foraging and vigilance, the tendency of individual predators to focus attention on searching for cryptic prey may be correlated with other behavioural traits which reflect risk-reward trade-offs, such as consistent inter-individual variation in boldness (a personality trait describing risk-taking, defined in this study as the time taken to leave a refuge). The aim of this study was to investigate the importance of personality in prey detection by comparing inter-individual variation in the response of three-spined sticklebacks (*Gasterosteus aculeatus*) to cryptic and conspicuous prey. Fish were slower to attack cryptic prey than conspicuous prey, consistent with cryptic prey being harder to detect. Despite the greater challenge involved in detecting cryptic prey, inter-individual variation in the time taken to detect prey was similar in the cryptic and conspicuous prey treatments, and was uncorrelated with boldness, which was repeatable between individuals. There was also a positive association between the rate of attack on conspicuous prey and whether individual fish attacked cryptic prey in other trials. These findings suggest that boldness is not related to prey detection or attention in this context. Instead, consistent differences in motivation between individual predators once exploration has begun may explain inter-individual variation in the time taken to attack both cryptic and conspicuous prey.

2.2 Introduction

Consistent differences in behaviour between individual predators are an important factor influencing predation risk, with the potential to shape ecological communities and maintain variation within prey populations (Pruitt, Stachowicz and Sih, 2012; McGhee, Pintor and Bell, 2013; Start and Gilbert, 2017). Most previous research on this personality variation in predators has concentrated on exploring the relationship between inter-individual differences in predator activity or boldness (i.e. tendency to take risks) and encounter rates with prey or the rate of prey consumption (Ioannou, Payne and Krause, 2008; Pruitt, Stachowicz and Sih, 2012; Michalko and Řežucha, 2018). However, after encountering prey, predators must first detect potential targets before they can approach, attack and eventually capture prey. Consequently, prey have evolved a range of camouflage strategies which allow them to evade detection by exploiting the sensory or cognitive systems of their predators (Skelhorn and Rowe, 2016). One of the most widespread camouflage strategies is background matching, which increases prey survival by achieving a close resemblance between the hue, brightness and pattern of a prey animal's body and a sample of the surrounding habitat (Endler, 1978; Troscianko *et al*., 2016), minimising the signal produced by the animal relative to noise from the background (Merilaita, Scott-Samuel and Cuthill, 2017). Inter-specific variation in predator visual systems has previously been linked to the effectiveness of different forms of cryptic colouration in prey (Stuart-Fox, Moussalli and Whiting, 2008). Within populations of the same predator species, individuals also differ in characteristics relevant to the detection of cryptic prey, such as their experience of searching for differently camouflaged prey types, their capacity to learn from experience, and their motivation to gather additional information about the profitability of certain prey types (Ehlinger, 1989; Sherratt, 2011). Despite the importance of consistent inter-individual behavioural variation as a factor influencing predation risk, little is known about the relationship between personality in predators and prey defences such as crypsis.

Boldness is a frequently studied personality trait which indicates a tendency to prioritise rewards over risks (Ward *et al*., 2004; Réale *et al*., 2007). Consistent inter-individual differences in boldness have been shown to affect the tendency to venture beyond the safety of cover (Pearish, Hostert and Bell, 2013; Schirmer *et al*., 2019), disperse more widely (Fraser *et al*., 2001) and are often highly correlated with other widely studied personality traits such as activity, aggressiveness or the propensity to explore a novel environment (Bell and Sih, 2007; Dingemanse *et al*., 2007; Sih and Bell, 2008; Quinn *et al*., 2012). This suggests that individual predators are likely to vary in the proportion of time they spend actively searching for prey, and the rate at which they encounter prey in their environment. In agreement with the expected effects of predator personality on encounter rates, the results of mesocosm study show that stable differences in the activity of individual predators can determine prey survival (Pruitt, Stachowicz and Sih, 2012). Although this study highlights the importance of predator activity levels and boldness in predicting the threat posed to prey, the relevance of such traits beyond the initial encounter stage remains unclear. While there is some evidence that predators exhibit consistent inter-individual differences in the speed with which they attack and their ability to capture prey (Exnerová *et al*., 2010; Smith and Blumstein, 2010; McGhee, Pintor and Bell, 2013), relatively little attention has been directed towards the possibility that individual predators differ in aspects of their behaviour which are relevant to other important stages of the predation sequence, including prey detection (Lima and Dill, 1990).

Detecting prey can be cognitively challenging when prey closely match the visual properties of the background. Locating prey in these conditions can involve intensive search effort, as demonstrated by evidence that predators concentrate their attention on particular prey types by forming search images for specific prey features (Langley *et al*., 1996; Bond and Kamil, 1999). Due to constraints on the capacity of animals to process information at any given instant, attention is regarded as a finite cognitive resource (Dukas, 2002). As a result, predators are less able to detect alternative prey when their attention is divided between searching for distinct prey types (Dukas and Kamil, 2001), or detect unexpected peripheral stimuli, such as an approaching predator, during difficult search tasks

(Dukas and Kamil, 2000). Limited attention is also thought to underpin the widely reported trade-off between foraging and anti-predator vigilance, which occurs when these activities cannot be performed simultaneously (Godin and Smith, 1988; Krause and Godin, 1996). Prey detection might therefore be influenced by the tendency of individual predators to redirect attention away from their own anti-predator vigilance and towards their efforts to locate prey, as well as factors affecting search tactics, such as the extent to which individuals relax their anti-predator vigilance as their search progresses (Ioannou, Ruxton and Krause, 2008). Since widely studied axes of behavioural variation such as the bold-shy continuum also reflect the priority given to resource acquisition over risk avoidance, personality traits such as boldness may be related to differences between individual predators in prey detection (Sih and Del Giudice, 2012).

Once predators are in the vicinity of prey, after an encounter has occurred, the capacity of individual predators to direct their attention towards the detection of prey is likely to be an important factor determining detection times. Conversely, for conspicuous prey which can be readily detected without much difficulty, attention should be less important and should play a reduced role. If driven by limited attention, any consistent differences between individual predators in prey detection should therefore only be apparent when prey are cryptic and not when prey are conspicuous against the background. Since variation in boldness reflects a continuum ranging from risk-prone (bold) to risk-averse (shy) behaviour, boldness may also be correlated with the tendency to re-focus attention away from anti-predator vigilance and towards the search for prey. Bold predators are therefore expected to detect cryptic prey more rapidly than shy individuals, but negligible, or reduced, differences between bold and shy individuals are expected when predators search for conspicuous prey. This should result in greater differences between individual predators in the time taken to detect cryptic prey, compared to the degree of inter-individual variation in the time taken to detect conspicuous prey.

To test these hypotheses, three-spined sticklebacks (*Gasterosteus aculeatus*) were repeatedly presented with conspicuous or cryptic prey items over the course of multiple trials, by manipulating the visual conspicuousness of prey relative to the background. This experimental approach has previously been shown to drastically reduce the probability of visual detection for cryptic prey by three-spined sticklebacks in trials in which fish were given a relatively short period of time to search for prey (Ioannou and Krause, 2009). This methodology was adapted by allowing fish to search for prey over a longer period and by repeatedly testing the same individuals, enabling the degree of inter-individual variation in the time taken to detect prey to be compared between trials with cryptic prey and trials with conspicuous prey. The design of the experiment also allowed the influence of boldness on inter-individual differences in the response of predators to cryptic and conspicuous prey to be examined. Boldness was quantified by measuring the time taken for individual fish to leave a refuge, as this measure has previously been shown to be repeatable in three-spined sticklebacks (Ioannou, Payne and Krause, 2008; Harcourt *et al*., 2009a; Ioannou and Dall, 2016), is correlated with other measures of risk-taking (Wilson *et al*., 2011), and most importantly, has a direct impact on foraging and predation risk (Orrock *et al*., 2013; Hulthén *et al*., 2017; Balaban-Feld *et al*., 2019a).

2.3 Methods

2.3.1 Experimental subjects and housing

Three-spined sticklebacks used in the study were caught from the River Cary, Somerset, UK on a single date in early November 2017, using large hand-nets dragged through vegetation. Of 275 fish initially caught for use in different behavioural experiments, 54 individuals were tested in this experiment (mean standard body length: 30.8 mm, standard deviation: 4.63 mm), and were haphazardly caught from this larger total. In the lab, fish were housed in glass tanks (width = 40 cm, length= 70 cm, height = 34 cm) with daily 13:11 dark:light cycle and water temperature maintained at 16 °C (+/- 0.5 °C). As these lighting and temperature conditions prevented the sticklebacks from entering a reproductive state, it was not possible to determine non-invasively the sex of the fish used in the experiment (Borg *et al*., 2004; Harcourt *et al*., 2009a; Ioannou and Dall, 2016). Throughout non-experimental periods, fish were fed defrosted bloodworms (Chironomidae larvae) once a day.

Experimental trials took place in November and December 2017, with a minimum of 5 days between fish being caught and the first fish being tested. During experimental periods, pairs of fish were transferred to breeding nets (width = 12 cm, length = 16 cm, height = 13 cm) consisting of a fine-meshed fish net material supported by a plastic frame. Breeding nets contained an artificial plant as a refuge and were positioned within one of the stock tanks. To ensure individual fish could be easily identified, fish were paired on the basis of differences in body size. To standardise hunger levels across individuals, fish were fed one bloodworm per day over the course of the experimental period after testing on that day. Once fed, fish did not have an opportunity to feed until the next trial, and as trials were performed one day apart, this is likely to have allowed sufficient hunger levels to build up between consecutive trials for fish to be motivated to search for prey when tested (Heller and Milinski, 1979; Salvanes and Hart, 1998; Harcourt *et al*. 2009b). After being tested in the experiment, fish were returned a separate glass tank (width = 40 cm, length= 70 cm, height = 34 cm) and kept isolated from untested fish to avoid retesting of the same individuals.

2.3.2 Experimental procedure

Experimental trials were conducted in four identical arenas (width = 40 cm, length = 60 cm, height = 18 cm; **Fig. 2.1**), filled with aged water to a depth of 10cm. Each arena was divided into two compartments: a covered refuge, and an uncovered zone which contained a feeding patch (a grid of alternating red and white squares). The covered refuge was separated from the uncovered zone by a white plastic barrier, with a retractable door situated within the barrier. Trials were filmed using a

GoPro Hero 5 video camera mounted above the arenas. The group of four experimental arenas were surrounded by white PVC sheeting, preventing disturbance to the fish during experimental trials.

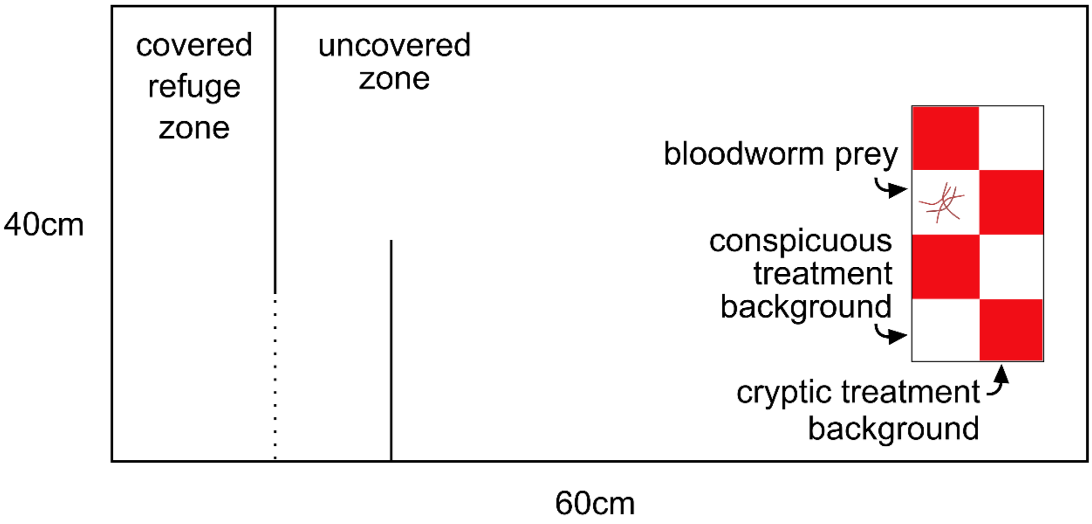

Figure 2.1: Top-down view of the experimental set-up used to examine the response of three-spined sticklebacks to conspicuous and cryptic prey. A retractable door situated within the barrier (dotted line) was used to habituate the fish in the refuge zone before allowing them access after the door was opened remotely. An additional barrier was positioned immediately in front of the door opening, preventing visual contact between the refuge and the feeding grid.

During experimental trials, the visual conspicuousness of prey was manipulated by placing four bloodworms on either a single white grid square (conspicuous treatment) or a single red grid square (cryptic treatment) before the start of each trial. In previous experiments using this methodology in which trials lasted 15 minutes, cryptic prey were almost never detected by three-spined sticklebacks when fish were given a relatively short period of time to search for prey (Ioannou and Krause, 2009). While olfactory cues are important in alerting sticklebacks to the presence of prey, experimental evidence suggests that visual cues are used to pinpoint the exact location of prey (Johannesen, Dunn and Morrell, 2012). Trials commenced when fish were transferred to the refuge and left to acclimatise for 5 minutes, after which the door to the uncovered zone containing the grid was opened remotely, and left open for the remainder of the trial (40 minutes).

Over the course of the experiment, individual fish were repeatedly tested: two trials with conspicuous prey and two trials with cryptic prey, resulting in four trials per individual. Trials were conducted once per day over a 5-day period, with a day-long gap separating blocks of two trials occurring on the first (trials 1 and 2) and last two days (trials 3 and 4). Treatments were pseudo-randomly assigned within two-day blocks such that each treatment occurred only once within trials 1 and 2, and only once in trials 3 and 4. When determining where to place prey items within each treatment, the choice of grid square was also pseudo-randomised: in trials 1 and 2, a grid square was randomly chosen from the row nearest to the refuge, and in trials 3 and 4 a grid square was randomly chosen from the row furthest from the refuge.

2.3.3 Video analysis

Three behavioural variables were extracted from video recordings of each experimental trial. The time taken to first leave the refuge was recorded as a measure of risk-taking tendency (i.e. boldness). Encounters with prey were defined as occurring when fish swam over the feeding grid, and the time taken to first encounter prey was the time difference between the instant the fish left the refuge and the point at which it first swam over the feeding grid. Attacks on prey occurred when fish consumed prey, and the time taken to attack was calculated in two different ways: either as the difference between the first encounter with prey and the point at which prey were first consumed, or the time difference between the fish leaving the refuge and when the fish began to consume prey. Two separate definitions of the time taken to attack were used in the analysis to test whether the results were sensitive to when an encounter with prey was considered to have occurred (visual contact with prey was possible from when fish first left the refuge, but prey detection was more likely when fish approached within a much closer range by directly swimming over the feeding grid). To minimize bias, video analysis was conducted blind to the identity of the individual fish.

2.3.4 Statistical analysis

All statistical analyses were conducted in R version 3.6.0 (R Development Core Team, 2019). The degree to which individual fish differed consistently in their risk-taking tendency (time taken to first leave the refuge) was assessed by estimating the adjusted repeatability of this trait, using a generalised mixed-effects modelling approach contained within the rptR package in R (Stoffel, Nakagawa and Schielzeth, 2017). In this context, the adjusted repeatability represents the proportion of the total phenotypic variance that can be attributed to individuals, excluding variation explained by fixed effect explanatory variables of trial number (i.e. 1 to 4) and standard body length (Nakagawa and Schielzeth, 2010). Trials in which individual fish failed to leave the refuge were disregarded from this stage of the analysis (22 out of 216 trials), in order to avoid influencing estimates of within-individual variation and thus affecting the resulting repeatability estimate (Stamps, Briffa and Biro, 2012). Statistical significance of the repeatability estimate was assessed using a combination of *P*-values obtained via a likelihood ratio test and the overlap of 95% confidence intervals with zero computed through parametric bootstrapping.

Data on the time taken to first encounter and attack prey included multiple censored observations, in which fish failed to either encounter (10 out of 194 trials in which fish left the refuge; conspicuous treatment: 8 out of 99 trials, cryptic treatment: 2 out of 95 trials) or attack the prey before a trial ended (102 out of 184 trials in which fish encountered prey; conspicuous treatment: 41 out of 91 trials, cryptic treatment: 61 out of 93 trials). Cox proportional hazards (PH) models were therefore used to analyse the effect of prey treatment and other explanatory variables on the time taken to first encounter or attack prey, using the coxme package in R (Therneau, 2018). This statistical approach is capable of handling truncated or censored observations, and enables the relationship between the explanatory variables and the hazard rate (in this context, the instantaneous rate at which prey are first encountered or attacked, given that the event has not yet occurred) to be examined, without making any assumptions about the precise shape of the baseline hazard function (Therneau and Grambsch, 2000). Random effect terms can also be incorporated within Cox PH models in order to account for non-independence arising from repeated observations from the same groups (in this case, individuals), and to describe variation between groups (or individuals) in the relative impact of the explanatory variables on the baseline hazard function (Austin, 2017). For all Cox PH models, the proportional hazards assumption was checked by inspecting plots of the Schoenfeld residuals, and the functional form of continuous explanatory was assessed by examining plots of these variables against the Martingale residuals (Moore, 2016).

The influence of prey treatment (conspicuous vs. cryptic) on the time taken to first encounter prey was examined by fitting a Cox PH model to data from trials where the fish had left the refuge (194 trials). Two separate Cox PH models were also constructed with the time taken to first attack prey as a response, in which this variable was defined either as the time difference between leaving the refuge and the attack (model a), or the time difference between the first encounter with prey and the attack (model b). Whereas model a was fitted to data from trials where fish had left the refuge (194 trials), model b was restricted to data from trials where fish encountered prey (184 trials). All models included prey treatment, the standard body length of each fish and the time taken for fish to first leave the refuge (during the same experimental trial) as explanatory variables and included an individual-level random effect. Since the inclusion of trial number as an explanatory variable was found to result in non-proportional hazards, models were also stratified by trial number. While inclusion of a stratified factor does not allow the effect of trial number to be estimated, it does enable the effect of trial number to be controlled for. Throughout the analysis, the statistical significance of explanatory variables was evaluated by using likelihood ratio tests to compare the full model (including all possible factors) to a reduced model lacking the variable in question. Hazard ratios and their 95% confidence intervals were also obtained by taking the exponential of model parameter estimates for fixed effects, to provide an indication of the relative impact of each explanatory variable on the rate of encounter or attack. Cumulative event curves were plotted using the survminer R package, and were based on the number of observed events (encounters or attacks) among individuals which had not yet encountered or attacked prey at each unique event time (Kassambra, Kosinski and Biecek, 2019).

To investigate the potential influence of prey treatment on the degree of inter-individual variation in the time taken to attack prey, data from the conspicuous and cryptic treatments were analysed separately. Standardised measures of inter-individual variation (e.g. the individual-level repeatability, or the proportion of behavioural variation that could be attributed to individuals) cannot be calculated from Cox PH models because the residual (i.e. within-individual) variance cannot be estimated. Instead, Cox PH models were used to obtain estimates of the variance associated with the individual-level random effect term, to provide an indication of the extent of inter-individual differences in the time taken to attack prey. Separate Cox PH models were therefore fitted to data from conspicuous and cryptic treatment trials, but as above, the time taken to attack was defined either as the time difference between leaving the refuge and an attack, or as the time difference between first encountering prey and an attack, resulting a total of four Cox PH models. All models included standard body length and the time taken to first leave the refuge (in the same trial) as explanatory variables, trial number as a stratification factor and an individual-level random effect. The statistical significance of the individual-level random effect was assessed using likelihood ratio tests comparing the integrated log-likelihood value (for a model with the random effect) to the partial log-likelihood of the model with the same fixed effect covariates but lacking the random effect term (Therneau and Grambsch, 2000; Moore, 2016). The uncertainty surrounding each estimate was reflected in 95% confidence intervals, obtained using a profile likelihood method (Therneau, 2018).

To investigate whether the ability of fish to detect cryptic prey was correlated with their response to conspicuous prey, additional Cox PH models were constructed to examine the relationship between behaviour during cryptic treatment trials and the time taken to attack prey in conspicuous treatment trials. As above, the time taken to attack was defined either as the time difference between leaving the refuge and an attack (model c), or as the time difference between first encountering prey and an attack (model d). Only a limited number of individuals attacked prey in both cryptic and conspicuous treatment trials. The behavioural response of fish to cryptic prey was therefore captured using a binary variable indicating whether or not individual fish attacked prey during any of the cryptic treatment trials. The model also included the standard body length of individual fish and the time taken for fish to first leave the refuge (in the same trial) as additional explanatory variables, trial number as a stratification factor and an individual-level random effect. Model c was fitted to data from conspicuous treatment trials in which fish left the refuge, and was additionally limited to individuals which had also left the refuge in at least one cryptic treatment trial (97 trials). Model d was restricted to conspicuous treatment trials in which fish encountered prey, and was additionally limited to individuals which had also encountered prey in at least one cryptic treatment trial, and therefore had the opportunity to attack cryptic prey (88 trials).

2.4 Results

2.4.1 Consistent inter-individual differences in boldness

Of the 54 fish tested, 53 individuals left the refuge in at least one experimental trial and 46 individual fish left the refuge in more than one experimental trial. In agreement with findings from previous studies on three-spined sticklebacks (Ioannou and Dall, 2016), the time taken to first leave the refuge was moderately repeatable ($R = 0.210$, 95% confidence intervals: 0.055-0.346, $P < 0.001$), demonstrating that individual fish consistently differed in their risk-taking tendency (boldness).

2.4.2 Differences in encounter and attack rates between the conspicuous and cryptic treatments

Among the 53 fish which encountered prey during at least one experimental trial by swimming over the feeding grid, only 37 individuals attacked prey in either the conspicuous or cryptic treatments. There was no effect of treatment on the time taken for fish to encounter prey once they had left the refuge (Cox proportional hazards model (Cox PH), 184 observed encounters in 194 trials where fish left the refuge: $\chi^2 = 0.115$, $P = 0.735$; **Fig. 2.2a**), suggesting that the time taken to reach the prey was not affected by any differences in the visual conspicuousness of prey between treatments. Fish were, however, significantly slower to attack cryptic prey compared to conspicuous prey. This was the case whether the time taken to attack was defined as the time difference between when the fish left the refuge and when an attack occurred (Cox PH, 82 observed attacks in 194 trials where fish left the refuge: $\chi^2 = 23.1$, $P < 0.001$; **Fig. 2.2b**), or whether it was defined with reference to the time at which prey were first encountered (Cox PH, 82 observed attacks in 184 trials where fish encountered prey: $\chi^2 = 18.5$, $P < 0.001$; **Fig. 2.2c**). Considering the model featuring the time taken to attack since fish emerged from the refuge (**Fig. 2.2b**), the rate at which cryptic prey were attacked was substantially reduced, approximately four-fold, relative to the rate of attack in trials with conspicuous prey (hazard ratio (HR) = 0.262, 95% confidence intervals: 0.149-0.460). Similar results were obtained from the model featuring the time taken to attack since prey were first encountered as the response variable (**Fig. 2.2c**, hazard ratio (HR) = 0.300, 95% confidence intervals: 0.176-0.514).

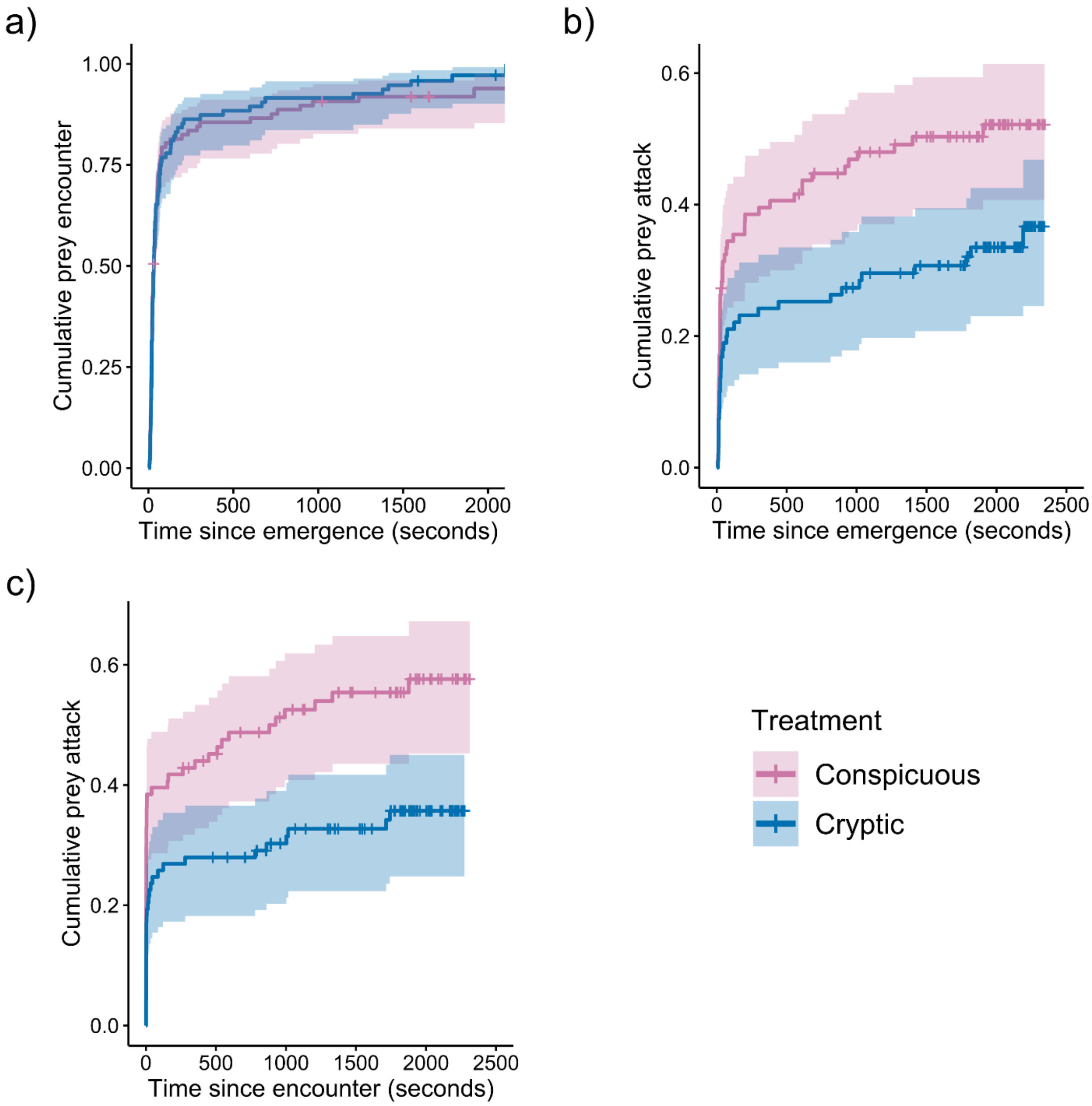

Figure 2.2: Cumulative event curves showing the effect of prey treatment (conspicuous vs. cryptic) on the probability that fish had encountered (a) or attacked prey (b, c), before a given time during an experimental trial. The time taken to first encounter or attack prey was calculated with reference to emergence from the refuge (a, b), and the time taken to attack was calculated using the first encounter with prey as the starting point (c). Shading surrounding the cumulative event curves indicates 95% confidence intervals. Crosses indicate experimental trials which ended before prey were encountered or an attack was made.

2.4.3 Inter-individual variation in attack rates

Individual sticklebacks differed in the time taken to attack prey, as demonstrated by the relatively poor performance of models lacking a random effect term for individual identity compared to the full model including the random effect, regardless of whether the time taken to attack was defined relative to emergence from the refuge (Cox PH: $\chi^2 = 79.5$, $P < 0.001$) or the point of encounter with prey (Cox PH: $\chi^2 = 59.0$, $P < 0.001$). To determine whether the degree of inter-individual variation in the time taken to attack prey was dependent on the type of prey encountered, data from the conspicuous and cryptic treatments were analysed separately. When the time taken to attack was defined from when fish left the refuge, including an individual-level random effect term significantly improved the model fit to a similar extent for both conspicuous (Cox PH, 50 observed attacks in 99 trials where fish encountered prey, no. of individuals = 52, $\chi^2 = 14.7$, $P < 0.001$) and cryptic treatments (Cox PH, 32 observed attacks in 95 trials where fish encountered prey, no. of individuals = 51: $\chi^2 = 10.8$, $P = 0.001$). Similar results were obtained when the time taken to attack was defined with respect to when fish first encountered prey (conspicuous treatment: Cox PH, 50 observed attacks in 91 trials where fish encountered prey, no. of individuals = 52, $\chi^2 = 8.99$, $P = 0.003$; cryptic treatment: Cox PH, 32 observed attacks in 93 trials where fish encountered prey, no. of individuals = 51: $\chi^2 = 11.6$, $P < 0.001$).

Model estimates of the variance associated with the individual-level random effect term also suggested that variation between individuals in the time taken to attack conspicuous prey was lower than the variation between individuals in the response to cryptic prey, regardless of the definition of the time taken to attack prey (**Table 2.1**). However, these estimates were associated with a high degree of uncertainty in both treatments as indicated by the wide and overlapping 95% confidence intervals, preventing any firm conclusions from being drawn on the question of whether inter-individual differences in the time taken to attack prey were more or less pronounced in either treatment. Additionally, there was no significant effect of the time taken to first leave the refuge (boldness) on the time taken to attack in either treatment, irrespective of whether this variable was defined relative to when fish first left the refuge (conspicuous treatment, Cox PH: $\chi^2 = 2.02$, $P = 0.155$; cryptic treatment, Cox PH: $\chi^2 = 1.25$, $P = 0.263$) or when prey were first encountered (conspicuous treatment, Cox PH: $\chi^2 = 0.73$, $P = 0.393$; cryptic treatment, Cox PH: $\chi^2 = 2.96$, $P = 0.085$).

Table 2.1: Estimated levels of inter-individual variation in the time taken to attack conspicuous and cryptic prey. Estimates represent the variance associated with individual-level random effects, derived from Cox PH models fitted to data from trials with cryptic or conspicuous prey. Figures in brackets denote the 95% confidence intervals surrounding each estimate.

Experimental treatment	**Estimated inter-individual variation in the time taken to attack prey**	
	Time taken to attack since first leaving the refuge	Time taken to attack since first encountering prey
Conspicuous	2.70 (0.77 - 7.66)	1.61 (0.34 - 4.96)
Cryptic	6.05 (0.99 - 18.5)	5.41 (1.09 - 21.5)

2.4.4 Relationship between the time taken to attack conspicuous prey and the response to cryptic prey

To explore the relationship between the behaviour of individual fish towards conspicuous prey and their response to cryptic prey, the effect of whether or not prey were attacked in any of the cryptic treatment trials on the time taken to attack conspicuous prey was also examined. Fish which attacked cryptic prey in at least one experimental trial were significantly quicker to attack conspicuous prey than those which never attacked the prey in any of the cryptic treatment trials, regardless of whether the time taken to attack was defined with respect to the moment fish first left the refuge (Cox PH, 50 attacks in 97 trials: $\chi^2 = 35.1$, $P < 0.001$; **Fig. 2.3a**) or the moment prey were first encountered (Cox PH, 49 attacks in 88 trials: $\chi^2 = 26.4$, $P < 0.001$; **Fig. 2.3b**). This is consistent with the interpretation that inter-individual variation in the time taken to attack prey was correlated across the two treatments.

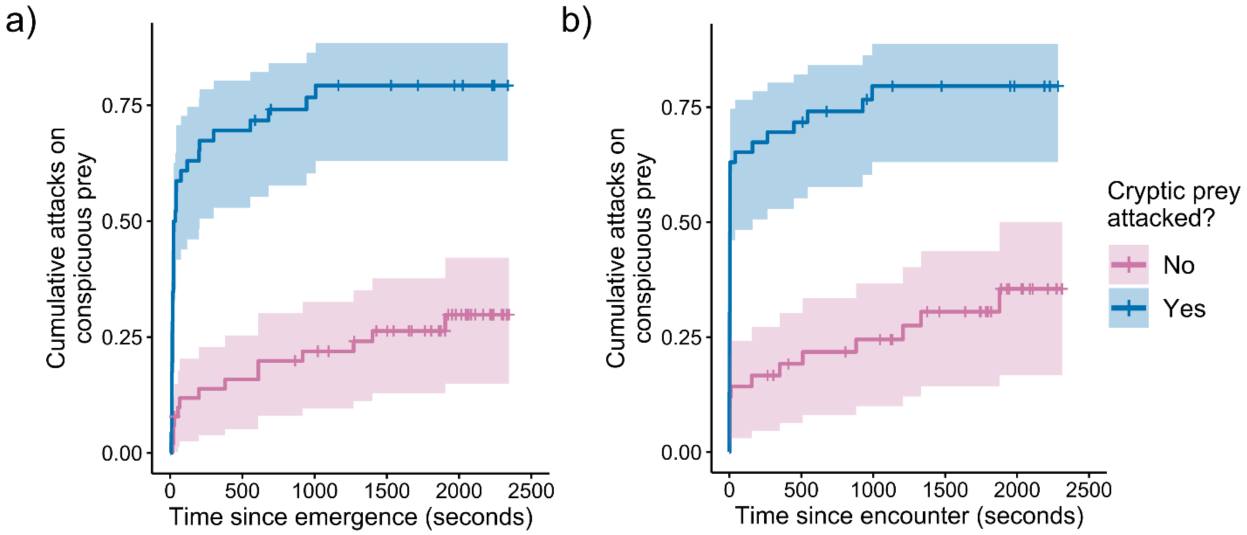

Figure 2.3: Cumulative event curves showing how the probability of attacking conspicuous prey before a given time during a trial is influenced by the behaviour of fish in trials with cryptic prey. The time taken to attack prey was defined with respect to the moment fish first left the refuge (a), or the instant fish first encountered prey (b). The blue and purple curves represent fish which attacked cryptic prey in at least one experimental trial (blue), and those which did not attack cryptic prey at all (red), respectively. Shading surrounding the cumulative event curve indicates 95% confidence intervals. Crosses indicate experimental trials which ended before prey were encountered or an attack occurred.

2.5 Discussion

In this experiment, fish were slower to attack cryptic prey than conspicuous prey, suggesting that prey matching their background were more difficult to detect (Ioannou and Krause, 2009). While individual sticklebacks consistently differed in the time taken to attack both cryptic and conspicuous prey, the degree of inter-individual behavioural variation was similar in the two treatments. If differences between individual predators had been driven by a trade-off between focusing limited attention on the search for prey versus anti-predator vigilance, greater variation would have been expected between individual fish in the time taken to attack cryptic prey compared to the response to conspicuous prey. Contrary to initial expectations based on previous work (Dukas and Kamil 2001; Ioannou, Payne and Krause, 2008), there was also no evidence for a correlation between the boldness of an individual three-spined stickleback (the time taken to first leave the refuge) and the time taken to attack either cryptic or conspicuous prey. These findings suggest that boldness (i.e. individual risk-taking tendency) is not correlated with prey detection in this context, and therefore may not be linked to attention or perceptual abilities. Rather than being influenced by boldness, the rate of attack on conspicuous prey was positively associated with whether individual fish attacked cryptic prey in other trials. The link between the behaviour of fish in trials with cryptic prey and the time taken to attack conspicuous prey suggests that variation in another unidentified individual-level trait may be more important in determining the behavioural response to both prey types.

One possible explanation for the absence of a relationship between boldness and the time taken to attack prey is that boldness levels determine how long it takes for a fish to leave a refuge, but the behaviour of a fish once it has left the refuge is uncorrelated with boldness. Instead of boldness, consistent differences in motivation between individuals might explain the behaviour of fish outside of the refuge, and could underpin inter-individual variation in the response of sticklebacks to both cryptic and conspicuous prey. Importantly, while differences in motivation between individuals can potentially account for inter-individual variation in the time taken to attack prey, motivational factors are unlikely to explain the longer time taken to attack cryptic compared to conspicuous prey. This is because average motivation levels should be the same in both treatments, as the two prey types only differed in their visual conspicuousness against a background. Other factors with the potential to affect risk-taking or the motivation to search for prey, such as the olfactory cues generated by prey, would also be expected to be the same in both treatments and to remain constant between trials. If inter-individual variation in the response to prey was driven by motivational differences, these results contrast with findings from previous work in which motivation was found to be correlated with boldness (Webster, Ward and Hart, 2009; Carter, Goldizen and Tromp, 2010; McDonald *et al*., 2016). These findings are also unexpected because of widespread evidence that inter-individual differences in measures of risk-taking, such as the time taken to leave a refuge, are related to other personality traits which are relevant to behaviour outside of a refuge (Sih and Bell, 2008). In many ecological contexts, widely studied personality traits such as boldness might not always be the most relevant axes of variation (Koski, 2014), and it may be important to consider factors such as motivation when attempting to use boldness to predict how individual predators will respond to prey. Differences in motivation between individuals could be driven by a range of factors, including short-term differences in hunger levels or physiological differences between individual fish, such as variation in metabolic rates. Although the pace-of-life syndrome hypothesis proposes that risk-taking is positively associated with higher metabolic rates and a fast life-history, the evidence for this relationship is mixed (Royauté *et al*., 2018), suggesting that there are many contexts in which boldness will not be correlated with energy intake and metabolic rates (Montiglio *et al*., 2018).

Although there were clear differences in the time taken to attack cryptic and conspicuous prey, it is possible that an effect of boldness was not observed because the task of detecting cryptic prey was not sufficiently challenging for trade-offs between foraging and vigilance to influence prey detection. An effect of boldness on the response of predators to cryptic prey may only become apparent when demands on attention are particularly acute. These conditions might arise when predators have an opportunity to form search images over successive encounters with prey, or are forced to divide their attention by searching for multiple distinct prey types (Dukas and Kamil, 2000; Dukas and Kamil, 2001). Similarly, an effect of limited attention on prey detection may only emerge when predators perceive themselves to be under greater threat from their own predators. During the saltatory, stop-start motion which is typical of a fish exploring its environment, previous studies have also demonstrated that boldness is negatively correlated with the length of pauses, and positively correlated with the speed and extent of rapid forward movements (Wilson and Godin, 2010). As visual perception may be inhibited during the rapid propulsive phase of intermittent locomotion (Kramer and McLaughlin, 2001), prey detection may also be compromised during these periods. Another possible explanation for these findings is therefore that the hypothesised positive effect of boldness on levels of attention directed towards searching and the negative effect of boldness on pause duration cancelled each other out, resulting in no overall effect of boldness on prey detection. Future studies may be able to arrive at a more comprehensive understanding of the links between boldness and prey detection by quantifying the movements and behaviour of predators in greater detail throughout the search process, up until the point when prey are attacked.

The impact of intra-specific variation in predator behaviour on diversity in prey visual defences has previously been explored in greater depth in the context of warning colours. For predators which are exposed to aposematic prey, learned associations between prey colour patterns and toxicity are generally thought to be maintained more readily for abundant prey phenotypes, resulting in positive frequency-dependent selection which favours monomorphic aposematic prey populations (Ruxton, Sherratt and Speed, 2004). There is however considerable evidence for polymorphism within aposematic species, and spatial variation in the composition of predator communities has been identified as a factor contributing to heterogeneity in selection pressures (Endler and Mappes, 2004; Nokelainen *et al*., 2014). Personality variation in avian predators has previously been shown to affect the degree of initial wariness displayed towards newly encountered aposematic prey, as well as the rate at which predators learned to avoid unpalatable prey types (Exnerová *et al*., 2010). If the expression of personality differences within predator populations is affected by local ecological conditions such as predation risk (Bell and Sih, 2007), any resulting differences in the distribution of personality types within predator populations might also lead to variability in selection on prey. By contrast, negative frequency-dependent selection by visual predators is recognised as having the potential to promote polymorphism in populations of cryptic prey, because predator search images provide a survival advantage to rare prey types (Bond and Kamil, 2002). Further work is required to clarify how variation in the tendency of individual predators to attack prey would affect patterns of variation within prey populations.

Beyond background matching, limited attention in predators may have implications for the strength of selection on a number of other prey traits, including other forms of defensive colouration and traits which influence collective behaviour. There is evidence to suggest that some camouflage strategies, such as disruptive colouration, are more effective at preventing improvements in prey detection with increasing experience than others which rely to a greater extent on preventing initial detection by naïve observers (Troscianko, Skelhorn and Stevens, 2018). Since selective attention plays a pivotal role in the formation of search images over repeated encounters with the same prey type, one untested possibility is that consistent differences between individual predators might have a greater impact on prey survival for some types of camouflage than others. Limits on attention in predators may also contribute to variability in how predators select for traits which influence both the composition and collective behaviour of prey groups. For predators which hunt groups of prey, successfully capturing a single individual from within the group can be challenging because it involves processing spatial information from multiple targets within the predator’s visual field (Krakauer, 1995). If the demands of tracking multiple prey exceed a predator’s limited capacity to process information, the resulting confusion effect can lead to a reduction in attack rates and a decline in the accuracy with which predators target individual prey (Ioannou *et al.*, 2008). Crucially, predators’ ability to overcome the confusion effect by focusing their attention on prey will depend on the costs associated with a reduction in their own anti-predator vigilance (Milinski and Heller, 1978; Milinski, 1984). If relaxing their own anti-predator vigilance is too costly, predators may switch to less cognitively demanding ways of countering confusion. These strategies might include concentrating attacks on prey close to the edge of the group where prey density is likely to be lower (Duffield and Ioannou, 2017), or preferentially targeting phenotypically dissimilar or “odd” prey within groups (Penry-Williams, Ioannou and Taylor, 2018). Future research should examine whether individual predators vary consistently in their response to camouflaged prey over successive encounters or differ in how they target individual prey within groups.

Chapter 3:

Predatory behaviour as a personality trait in a wild fish population

Still image from a video recording showing a pike cichlid (*Crenicichla frenata*) approaching a stimulus guppy shoal in a natural pool in the Lopinot river, Trinidad. Photograph: A. W. Szopa-Comley.

An adapted version of this chapter has been published as a pre-print and as a journal article:

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I designed the study, carried out data collection, analysed video recordings, conducted the statistical analysis and wrote the paper, in discussion with my supervisor Christos C. Ioannou. Callum Duffield and Indar W. Ramnarine assisted with data collection in the field.

3.1 Abstract

Consistent inter-individual differences in behaviour (i.e. animal personality variation) can influence a range of ecological and evolutionary processes, including predation. Variation between individual predators in commonly measured personality traits, such as boldness and activity, has previously been linked to encounter rates with their prey. Given the strong selection on predators to respond to prey, individual predators may also vary consistently in their response to prey in a manner that is specific to the context of predation. By observing the response of wild piscivorous fish (pike cichlids, *Crenicichla frenata*) to experimental presentations of prey and control stimuli in their natural environment, this study demonstrates that individual predators differ consistently in the amount of time spent near prey. Crucially, these differences were not explained by the behaviour of the same individuals in control presentations (the same apparatus lacking prey), suggesting that variation in the response to prey reflects a predation-specific personality trait which is independent from other individual traits (body size, boldness and/or neophobia) and environmental factors. Pike cichlids which spent more time near prey also attacked prey at a higher rate, suggesting that these individuals were more motivated to attack prey. These findings imply that the likely risk posed by individual predators cannot always be adequately predicted from typically studied axes of personality variation, and highlight the importance of considering inter-individual variation in more ecologically relevant traits.

3.2 Introduction

Through their direct effect on prey abundance (Paine, 1966) and non-lethal impact on prey physiology and behaviour (Beckerman, Uriarte and Schmitz, 1997; Lima, 1998), predators exert a strong influence on the structure and composition of ecological communities (Schmitz, Krivan and Ovadia, 2004). An extensive body of research has explored how prey adjust their behaviour in response to changes in predation risk (Lima and Dill, 1990), and has revealed how the mere presence of nearby predators can shape prey population dynamics and the abundance of resources at lower trophic levels (Preisser, Bolnick and Benard, 2005; Peckarsky *et al*., 2008; Suraci *et al*., 2016). Predators, by contrast, are often viewed as being behaviourally unresponsive, posing a fixed and uniform level of risk to prey (Lima, 2002). Increasingly this simplifying assumption is at odds with the evidence for widespread consistent inter-individual differences in behaviour (also known as personality variation) within natural populations (Bell, Hankison and Laskowski, 2009). As the effects of variation within species on ecological processes can often equal or outweigh the impact of differences between species (Des Roches *et al*., 2018), determining how individual predators differ in their behaviour is key to understanding their wider effects (Ioannou, Payne and Krause, 2008; Okuyama, 2008; Start and Gilbert, 2017; Michalko and Řežucha, 2018; Rhoades, Lonhart and Stachowicz, 2019).

Empirical research has shown that inter-individual behavioural differences can influence numerous ecological and evolutionary processes (Dall *et al*., 2012; Sih *et al*., 2012), ranging from dispersal (Cote *et al*., 2010) to pair bonding (Firth *et al*., 2018). However, most studies have focused on a limited number of traits, particularly boldness, exploration, activity, aggressiveness and sociability (Réale *et al*., 2007), which are not necessarily the most ecologically relevant axes of variation (Koski, 2014). Although a wide variety of other behaviours are known to be individually repeatable (reviewed in Bell, Hankison and Sih, 2009), there have been few tests examining whether inter-individual variation in these behavioural traits is separate from, or correlated with, frequently measured axes of variation. If commonly studied personality traits are not strongly correlated with other repeatable behaviours that have greater ecological or evolutionary relevance, this has implications for both how personality traits affect ecological and evolutionary processes, as well as the selection imposed on different personality traits. Answering this question may be particularly important for widespread ecological processes like predation, which is almost ubiquitous in animals across a diverse range of taxa and habitats.

The majority of studies exploring the consequences of personality differences for predator-prey interactions have concentrated on variation in activity levels or boldness (Bell and Sih, 2007; Pruitt, Stachowicz and Sih, 2012), behaviours which reflect the degree to which individuals prioritise gaining resources over risk avoidance (Smith and Blumstein, 2008). Bolder or more active prey are often more susceptible to predation (Griffen, Toscano and Gatto, 2012; Ballew, Mittelbach and Scribner, 2017; Hulthén *et al*., 2017), although this does not necessarily result in negative correlations between boldness and survival, particularly if bold individuals can avoid or offset the costs of predation by acquiring more resources (Moiron, Laskowski and Niemelä, 2020). The link between these traits and individual movement patterns also suggests that bolder or more active predators are also more likely to encounter prey (Spiegel *et al*., 2015). Consistent with the expected effect of boldness on encounter rates, the interacting effects of prey and predator behavioural types has been shown to determine prey survival (Pruitt, Stachowicz and Sih, 2012; Chang *et al*., 2017). In seabird populations, boldness also predicts inter-individual variation in how individual predators search for prey (Patrick, Pinaud and Weimerskirch, 2017), and as well as affecting encounter rates with prey, personality variation influences the rate of prey consumption (Toscano and Griffen, 2014). While individual predators have also been shown to differ consistently in their foraging patterns (Woo *et al*., 2008; Patrick *et al*., 2014; Nakayama, Rapp and Arlinghaus, 2016), including the time taken to detect, respond to or capture prey (McGhee, Pintor and Bell, 2013; Alcalay, Scharf and Ovadia, 2015; MacGregor, Herbert-Read and Ioannou, 2020), few studies have directly addressed whether frequently studied personality traits such as boldness predict the behavioural response of individual predators to their prey, once prey have been encountered.

When studying how individual predators vary in their response to their prey, quantifying predator behaviour in the wild can help avoid artefacts which arise when behaviour is expressed in laboratory conditions (Niemelä and Dingemanse, 2014). Predator personality variation will also be most relevant to the risk prey experience when prey are repeatedly exposed to the same individual predators. One system in which these conditions prevail are populations of the Trinidadian guppy (*Poecilia reticulata*) in their natural habitats, where guppies can be confined to the same natural river pools during the dry season as pike cichlids (*Crenicichla frenata*), their main predator (Magurran, 2005; Botham *et al*., 2006). Rather than engaging in lengthy pursuits, pike cichlids typically track their prey visually before attacking in a rapid burst once they have approached within close proximity (Walker *et al*., 2005; Heathcote *et al*., 2020).

In this study, inter-individual variation in the behaviour of pike cichlid predators was quantified by repeatedly presenting stimulus shoals of guppies *in situ* (the prey treatment) over multiple days across discrete natural river pools. Similar methods of quantifying predation risk have also been shown to correlate with anti-predator behaviour in this system (Croft *et al*., 2006). Importantly, the same apparatus without prey was also repeatedly presented as a control treatment in each pool. The response of individual predators to the control should reflect variation in the individual traits or environmental factors which are not specific to prey, including personality variation in boldness and neophobia (during the initial presentation, the (empty) stimulus was entirely novel). For example, whether or not individual pike cichlids were recorded approaching the control stimulus should indicate their response to novel features within their environment. By comparing the predator's behaviour in the prey and control treatments, it was therefore possible to isolate inter-individual variation in predatory behaviour (i.e. the response to prey) from factors that are not specific to prey. If personality variation in boldness or neophobia predicts the response of individual pike cichlids to their prey, inter-individual differences in the time spent near the stimulus during the prey treatment should be explained by the behaviour of the same individuals in the control. Conversely, if the response of individual predators to their prey was independent from boldness or neophobia, inter-individual differences in the time spent near the prey treatment stimulus should be uncorrelated with the behaviour of the same predators during control treatment presentations.

3.3 Methods

3.3.1 Study Site

Pike cichlids were studied in a series of discrete natural river pools in the Lopinot valley, Trinidad (see Appendix, Supplementary Table 1 for further details of the locations used). Pools in this river are characterised by deeper areas of water (>0.5m in depth), bounded by shallower sections containing riffles, rocks, boulders and small waterfalls which restrict the movements of fish. Other, although minor, predators known to be present in this river include blue acara cichlids (*Aequidens pulcher*), two-spot astyanax (*Astyanax bimaculatus*) and wolf-fish (*Hoplias malabaricus*) (Magurran, 2005).

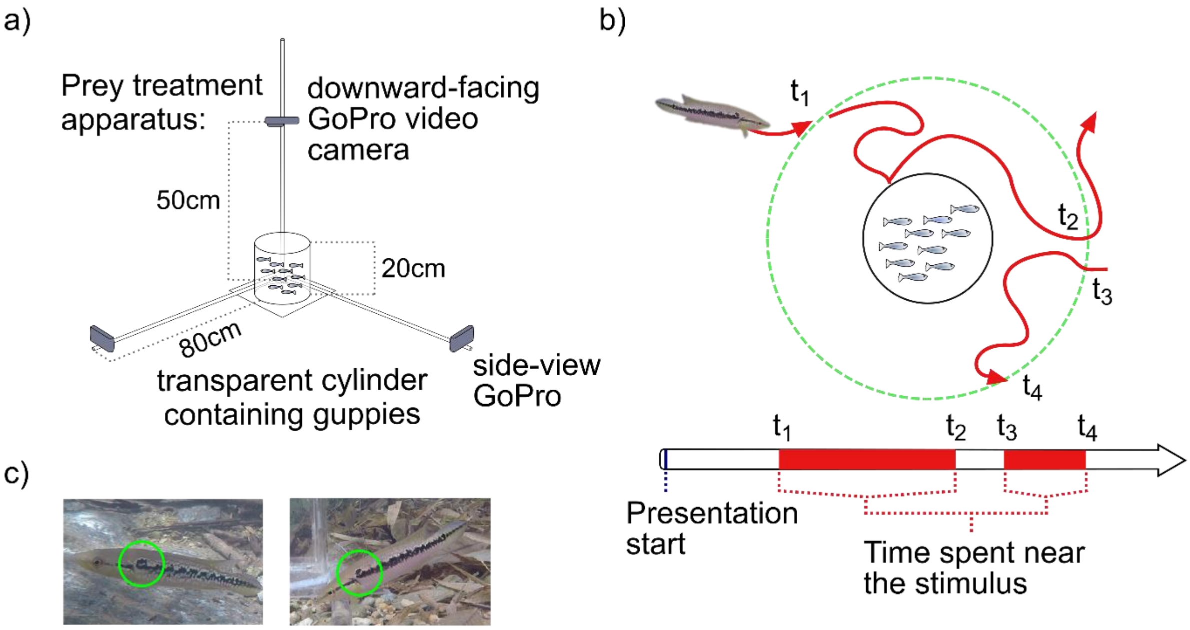


Figure 3.1: Quantifying inter-pool and inter-individual variation in predatory behaviour. (a) For each river pool, the apparatus used in the study was deployed in one of two treatments: in the prey treatment, 10 female guppies were placed within the cylinder (diagram not to scale), or in an otherwise identical control apparatus without guppies (not shown). (b) Depending on the level of the analysis (inter-pool or inter-individual differences), the time spent near the stimulus was defined as the total amount of time in which any pike cichlid (or a specific individual) was present within a zone surrounding the stimulus during the 30-minute presentation period. The green dashed line (approximately 24 cm from the outer edge of the cylinder) represents the outer limit of the zone surrounding the stimulus, viewed from above. The total time spent near the stimulus in each presentation is the sum of the time difference between t_1 and t_2 plus the time spent within the zone during subsequent approaches (denoted by t_3 and t_4, etc.). (c) Individual pike cichlids were identified through differences in humeral spot patterns (highlighted by green circles), using still images recorded by the side-view GoPro video cameras.

3.3.2 Experimental apparatus

The apparatus consisted of a transparent acrylic plastic cylinder (diameter: 15 cm, height: 20 cm, wall thickness: 3 mm) attached to a square base and covered by a perforated lid (**Fig. 3.1a**). Approaches to the apparatus were recorded using Go Pro video cameras attached to the ends of three clear acrylic plastic rods (diameter: 3 cm, length: 80 cm) secured to the base of the apparatus, with one rod extending vertically and two identical rods projecting horizontally at right angles to one another. This arrangement allowed footage of approaching fish to be captured from above (Hero 3+ video camera, frame rate: 25 frames per second, resolution: 960 p) and from the side (two GoPro Hero 5 video cameras, frame rate: 30 frames per second, resolution: 2.7 k; diagonal field of view for both camera models: 133.6°). The apparatus was manoeuvred into position from the edge of each pool with minimal disturbance using transparent monofilament attached to the base.

3.3.3 Experimental Procedure

The study was designed to quantify inter-individual differences in the behavioural response of predators to their prey by repeatedly presenting a stimulus prey shoal (the prey treatment, consisting of 10 female guppies placed within the cylinder of the apparatus) to free-swimming predatory fish in their natural environment. Control presentations of an otherwise identical apparatus without guppies were also conducted in the same locations to measure variation in the individual traits of the same predator individuals (such as personality variation in boldness and neophobia) which have been shown to influence encounter rates with prey (Pruitt, Stachowicz and Sih, 2012). With this approach, it was then possible to test for the existence of a separate predator personality trait by examining individual responses to prey and responses of the same individuals when prey were absent.

Experiments were carried out over a six-week period from March to May 2017. At the start of each 30-minute long presentation period, the apparatus was placed in the same location and orientation within each pool. For each river pool, the apparatus used in the study was deployed in one of the two treatments in six separate presentations (once per day): three prey treatment presentations and three control presentations. Presentations took place between 0730 and 1130 over a period of six consecutive days. Within each six-day period, control presentations of the entirely novel apparatus always took place on the first day. Guppies used in prey treatment presentations were caught from a single pool in the same river using a seine net (the stimulus was not deployed in this pool). In each prey treatment presentation, 10 female guppies of a similar size were selected haphazardly from a number collected at the start of each day. The order in which the two treatments were assigned to the remaining five presentations per pool was randomised, but for logistical reasons, the three pools tested over the same six-day period shared the same presentation order. As incident light levels may affect pike cichlids' ability to detect prey (Endler, 1987), pool canopy openness was also measured after completion of the experiment by averaging measurements taken with a spherical densiometer in all four cardinal directions at three points along at the pool's upstream-downstream axis: the upstream end, midpoint and downstream end (Schwartz and Hendry, 2010).

3.3.4 Video Analysis

Data on the behavioural response of pike cichlids in each pool were extracted manually from videos at two levels: pool-level data on the time spent near the stimulus by any predator individual over the course of the 30 minute presentation period, and individual-level data on the time spent near the stimulus by individual pike cichlids. In both the pool- and individual-level analyses, the time spent near the stimulus was defined as the total amount of time in which any pike cichlid (or a specific individual) was present within a zone surrounding the stimulus during the 30 minutes presentation period (the zone extending to approximately 24 cm from the outer edge of the cylinder; **Fig. 3.1b**).

Attacks on the stimulus were defined as fast, directed movements towards the apparatus. Whether or not individual pike cichlids attacked the apparatus during a presentation was noted after watching each video. The number of attacks made by an individual during the first 30 seconds of a presentation was also recorded, resulting in a measure of the initial attack rate. The number of pike cichlids in each pool was estimated using still images recorded using the side-view cameras (fish which could not be conclusively identified were not included in this total). The standard body length of individual pike cichlids (median approximate standard body length: 9.8 cm, inter-quartile range: 2.9 cm) was quantified in ImageJ (version 1.46r) using still images obtained from the downward-facing video camera (**Fig. 3.1c**) and comparing fish-length measurements in pixels to an object of known length (the stimulus cylinder viewed from above).

3.3.5 Statistical Analysis

All analyses were carried out using R v. 3.3.2 (R Development Core Team 2019), and all LMMs (linear mixed effects models) and GLMMs (generalised linear mixed effects models) were fitted with the lme4 package. Prior to model fitting, all continous explanatory variables were standardised by subtracting the mean and dividing by the standard deviation. In each model, *P*-values for fixed effects were derived from likelihood ratio tests comparing the full model with a reduced model lacking the variable in question. Throughout the analysis, LMM assumptions were verified by inspecting Q-Q plots of residuals (to check the assumption of normality of the residuals was met) and plots of residuals versus fitted values (to check for homoscedasticity of the residuals). The corresponding checks for GLMMs were performed using the DHARMa R package (Hartig, 2020), in addition to checks for over-dispersion. Results and further details for all models are given in the Appendix, Supplementary Table 2.

Before quantifying inter-individual differences in predatory behaviour, Poisson GLMMs were first used to determine whether the time spent near the stimulus by pike cichlids differed between prey treatment and control presentations (models 1-2 in Appendix, Supplementary Table 2). Models were fitted to data at the level of a given presentation (211 observations) for all individual pike cichlids observed approaching the apparatus (69 individuals). Two separate Poisson GLMMs were constructed featuring either presentation number (i.e. 1 to 6, included to account for any habituation or learning effects) or the proportion of previous prey treatment presentations as fixed effects (capturing variation in the sequence in which control and prey stimuli were presented). Calculation of variance inflation factors (VIFs) revealed substantial collinearity between these two explanatory variables, preventing them from being included within the same model, in order to avoid problems associated with collinearity (Graham, 2003; Zuur, Ieno and Elphick, 2010). Both models included the following additional fixed effects: treatment (control vs. prey treatment), time of day (to account for the effects of diurnal cycle on pike cichlid behaviour [Endler, 1987]), canopy openness (levels of incident light may affect visibility and therefore predator-prey interactions) and the estimated number of pike cichlids in each pool (obtained from video analysis). Pool and individual identity were included as nested random intercepts in both models, to account for non-independence arising from repeated measures of the same individuals and clustering of multiple individuals within each pool. Observation-level random intercepts were also included within both models to counter over-dispersion (Harrison, 2014).

Additional models (models 3-6 in Appendix, Supplementary Table 2) were also constructed in order to determine whether the amount of time an individual pike cichlid spent near the stimulus during a given presentation was associated with the tendency to attack the stimulus during the same presentation. Binomial GLMMs were first used to evaluate the effect of the time spent near the stimulus on the probability of an attack occurring at some point during a presentation. As no attacks on the stimulus occurred during control presentations, this analysis was restricted to prey treatment presentations (133 observations of 68 individuals). Poisson GLMMs were subsequently used to determine the relationship between the time spent near the stimulus and the number of attacks made during the first 30 seconds of a presentation. These models were fitted to data from prey treatment presentations in which pike cichlids spent a minimum of 30 seconds near the stimulus (123 observations of 63 individuals). Time of day, canopy openness and the estimated number of pike cichlids in each pool were also included as fixed effects in all of the models used to analyse pike cichlids' attack behaviour. As above, separate models were constructed featuring either presentation number (i.e. 1 to 6) or the proportion of previous prey treatment presentations as an explanatory variable. Pool and individual identity were included as nested random intercepts in both models.

To quantify inter-individual differences in predatory behaviour, estimates of adjusted repeatabilities and inter-individual variances were obtained using the rptR package (Stoffel, Nakagawa and Schielzeth, 2017), which utilises a mixed model framework (Nakagawa and Schielzeth, 2010), allowing experimental (presentation number and time of day) and environmental variables (canopy openness and the estimated number of pike cichlids in each pool) to be included as fixed effects. Adjusted repeatabilities can thus be interpreted as a standardised measure of inter-pool or inter-individual variation after potentially confounding variables have been controlled for. LMMs were used to analyse pool-level data and Poisson GLMMs were used to analyse individual-level data, which also included an approximate measure of pike cichlids' standard body length as an additional fixed effect to control for predator body size. Pool identity was included as a random intercept in models used to analyse pool-level data. Models used to analyse individual-level data included both pool and individual identity as nested random intercepts. Pool identity was included in these models to control for any unmeasured differences in the pool environment which remained consistent over the length of the study. Statistical significance of repeatability estimates was assessed using both *P*-values (obtained through likelihood ratio tests) and overlap of the 95% confidence intervals with zero (computed via parametric bootstrapping). Data on the time spent near the stimulus was censored at a maximum of 30 minutes corresponding to the duration of a presentation, but no fish spent the maximum amount of time near the stimulus. Unless otherwise stated, instances when fish spent zero time near the stimulus were disregarded in the analysis in order to avoid influencing estimates of within-pool or within-individual variation and thus affecting repeatabilities (Stamps, Briffa and Biro, 2012).

Studies quantifying personality differences in the field can be biased if individuals with a certain behavioural type are predisposed to interact with the behavioural tests or stimuli which are presented (Stuber *et al.*, 2013). To ascertain the potential for sampling bias in this study, a Poisson GLMM (Appendix, Supplementary Table 2, model 7) was used to determine whether the initial response of pike cichlids to their prey was dependent on the number of prey treatment presentations in which an individual predator had approached the stimulus. This model included the time spent near the stimulus during the first prey treatment presentation that an individual was observed in as the response variable. The model was fitted to data on the response of all individual pike cichlids which approached the stimulus during at least one prey treatment presentation (68 individuals). Pool and individual identity were included in the model as nested random intercepts, and an observation-level random intercept term was also included to counteract over-dispersion (Harrison, 2014).

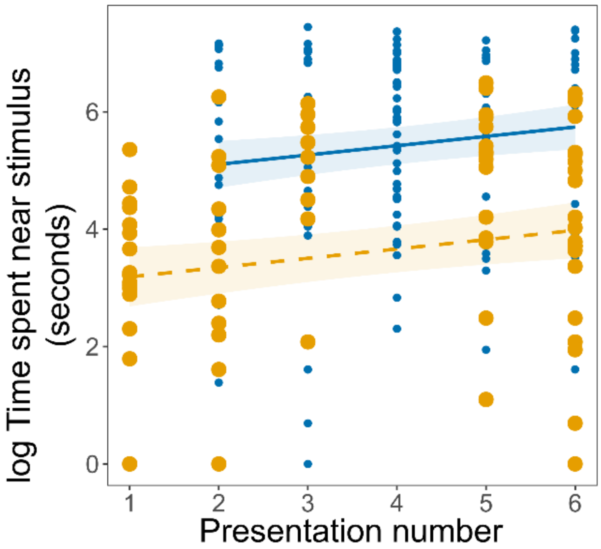
Social interactions between predators within the same pool also have the potential to generate feedbacks which magnify (via differentiation) or suppress (via conformity) inter-individual differences in behaviour (Webster and Ward, 2011). To test for these possibilities, two types of randomisation simulations were conducted based on data for predators which approached the prey treatment stimulus in multiple presentations (44 individuals), following the methodology outlined in Ioannou, Ramnarine and Torney (2017). In the first randomisation, the mean observed pool-level diversity in the response to prey between predators across all pools was compared to the distribution of this statistic produced when the set of observations corresponding to an individual predator was randomly exchanged between pools. The aim of this approach was to determine whether the response of individual predators to prey was dependent on the other individuals present within the same pool, or whether being in a particular pool is statistically unimportant. Pool-level diversity in the response to prey was quantified as the coefficient of variation (COV) in the time spent near the prey treatment stimulus. The second randomisation examined the relationship between the time spent near the stimulus by two individuals (‘predator 1’ and ‘predator 2’) which were randomly selected (without replacement) from the same pool. To enable direct comparison of the response to prey by ‘predator 1’ and ‘predator 2’, observations were selected from the same presentation per pair. Across multiple pools, a negative slope would be expected from behavioural differentiation between the two individuals (if one predator spends a long time near the stimulus, the other does not), whereas a positive slope would be consistent with conformity (both ‘predator 1’ and ‘predator 2’ spend a similar amount of time near the stimulus). The slope of the relationship between time spent near the stimulus by ‘predator 1’ and ‘predator 2’ was estimated using a quasi-Poisson generalised linear model, controlling for variation between pairs in presentation number, time of day, canopy cover and the estimated number of pike cichlids in each pool by including these variables as main effects. Both randomisation procedures were run with 10,000 iterations.

Several LMMs were also constructed to examine the relationship between the time pike cichlids spent near the stimulus and the behaviour of the same individual predators during control presentations. Models were initially used to explore the effect of the mean time spent near the stimulus across all three control presentations (Appendix, Supplementary Table 2, model 8), or the time spent near the stimulus in the first control presentation in which an individual was observed (indicative of responses to the novel apparatus; Appendix, Supplementary Table 2, model 9), on the time spent near the stimulus during prey treatment presentations. These models were fitted to data on individual predators which approached the stimulus in two or more prey treatment presentations, and which were also observed approaching the stimulus in at least one control treatment presentation (87 observations of 35 individuals). Additional models were fitted to investigate whether the time spent near the stimulus during prey treatment presentations was influenced by whether or not an individual pike cichlid was observed in any (Appendix, Supplementary Table 2, model 10) or the first of three (Appendix, Supplementary Table 2, model 11) control treatment presentations. These models were fitted to data on the response of individual pike cichlids which approached the stimulus in two or more prey treatment presentations (109 observations of 44 individuals).

3.4 Results

3.4.1 Responses to the experimental apparatus

A total of 69 individual pike cichlids were observed approaching the stimulus during at least one 30-minute presentation period (Appendix, Supplementary Table 1). Compared to their behaviour in control presentations, pike cichlids spent more time near the stimulus when prey were present (Poisson generalised linear mixed effects model (GLMM), N_{obs} (no. of observations) = 211, N_{ind} (no. of individuals) = 69: $\chi^2_1 = 63.2$, $P < 0.001$; **Fig. 3.2** and Appendix, Supplementary Table 2, model 1). Pike cichlids also spent more time near the stimulus with increasing presentation number (Poisson GLMM, $N_{obs} = 211$, $N_{ind} = 69$: $\chi^2_1 = 7.30$, $P = 0.007$; **Fig. 3.2**), indicative of habituation to the apparatus and presentation procedure. Attacks on the stimulus, defined as a fast, directed movement towards the apparatus, were only observed in prey treatment presentations. Pike cichlids which spent more time near the stimulus were more likely to attack the stimulus during the same presentation (binomial GLMM, $N_{obs} = 133$, $N_{ind} = 68$: $\chi^2_1 = 41.1$, $P < 0.001$; **Fig. 3.3a**; Appendix, Supplementary Table 2, model 3), and made more attacks during the first 30 seconds that they spent near the stimulus (Poisson GLMM, $N_{obs} = 123$, $N_{ind} = 63$: $\chi^2_1 = 6.83$, $P = 0.009$; Fig. **3.3b**; Appendix, Supplementary Table 2, model 5).



<u>Figure 3.2:</u> Relationship between log-transformed time spent near the stimulus and presentation number, in control (large orange points, dashed orange line) and prey (small blue points, solid blue line) treatment presentations. Shading represents 95% confidence intervals surrounding the predicted response derived from a GLMM featuring the time spent near the stimulus as the response (Appendix, Supplementary Table 2, model 1), with all other fixed effects not plotted above held constant at their mean values.

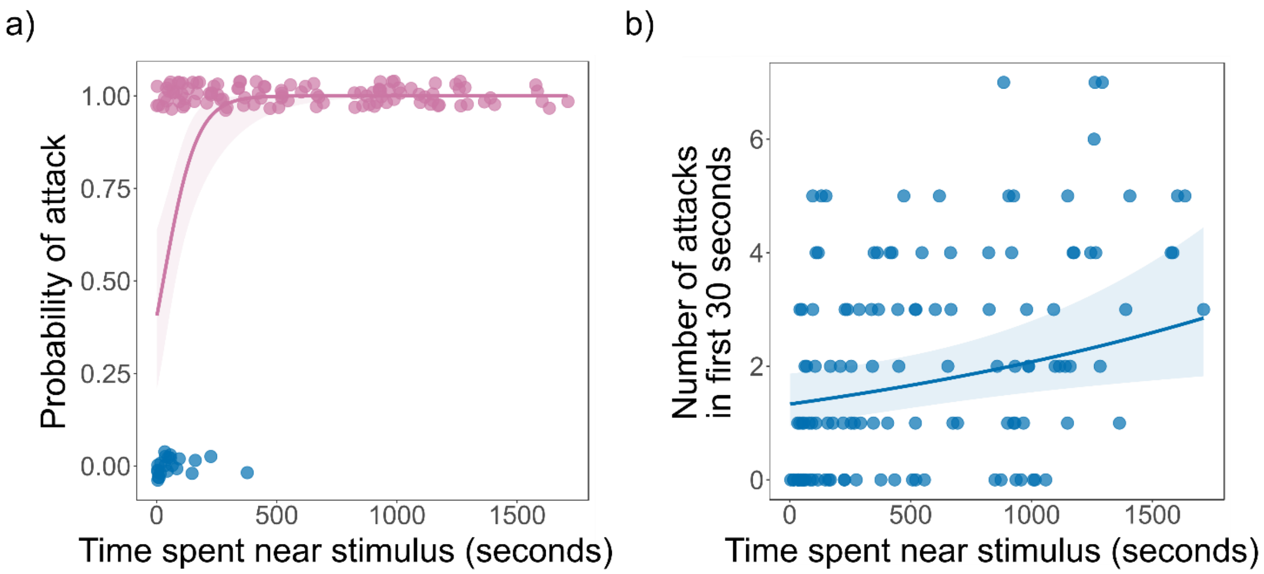


Figure 3.3: Relationship between the time spent near the stimulus and the attack behaviour of pike cichlids. (a) Probability of attack as a function of the time spent near the stimulus. Jitter has been added to the raw data to allow overlapping points to be visualised. (b) Relationship between the number of attacks made by pike cichlids during the first 30 seconds they spent near the stimulus and the total time spent near the stimulus during each presentation (this analysis was limited to pike cichlids which spent a minimum of 30 seconds near the stimulus). In both (a) and (b), curves represent the predicted response from a generalised linear mixed-effects model (GLMM): a binomial GLMM featuring attacks on the stimulus as a binary response variable in (a) and a Poisson GLMM in (b). Model predictions were obtained by holding all other fixed effects constant at their mean values. Shading indicates 95% confidence intervals surrounding the predicted response.

3.4.2 Local variation in predation risk between river pools

From the prey's perspective, the repeatability of predation risk in their local habitat (pools in this study) will be more relevant to the risk they experience than repeatable differences between individual predators. To address local variation in predation risk between river pools, inter-pool differences in the time spent near the stimulus by any pike cichlid in a given pool were quantified by estimating adjusted repeatabilities (Nakagawa and Schielzeth, 2010), controlling for variation arising from the experimental design (time of day and presentation number) and environmental differences between the pools (the estimated number of pike cichlids in each pool and canopy openness). Significant repeatability at the level of the pool was evident during prey treatment presentations, even when controlling for the estimated number of pike cichlids, i.e. predator density, in each pool (R_{pool} = 0.476, 95% confidence intervals: 0.093 - 0.759, P = 0.009, N_{obs} = 45, N_{pool} (no. of pools) = 16; **Fig. 3.4**, **Table 3.1).** The time spent near the stimulus by pike cichlids was not repeatable during control presentations without prey (R_{pool} = 0, 95% confidence intervals: 0 - 0.417, P = 1, N_{obs} = 35, N_{pool} = 15; **Fig. 3.4**, **Table 3.1**).

Table 3.1: Adjusted repeatability estimates (R_{pool}) indicating the extent of consistent inter-pool differences in the time spent near the stimulus, in both prey treatment and control presentations. The statistical significance of each estimate was assessed using a combination of P-values (obtained through likelihood ratio tests) and overlap of the 95% confidence intervals with zero (computed via parametric bootstrapping, denoted in square brackets). N_{obs} and N_{pool} refer to the number of observations and pools used in these analyses, respectively.

Variables controlled for	**Treatment**	N_{obs}	N_{pool}	R_{pool}	***P*-value**
time of day, presentation number	Control	35	15	0.007 [0, 0.462]	1
	Prey treatment	45	16	0.605 [0.258, 0.828]	< 0.001
time of day, presentation number, no. of pike cichlids in each pool, canopy openness	Control	35	15	0 [0, 0.417]	1
	Prey treatment	45	16	0.476 [0.093, 0.759]	0.009

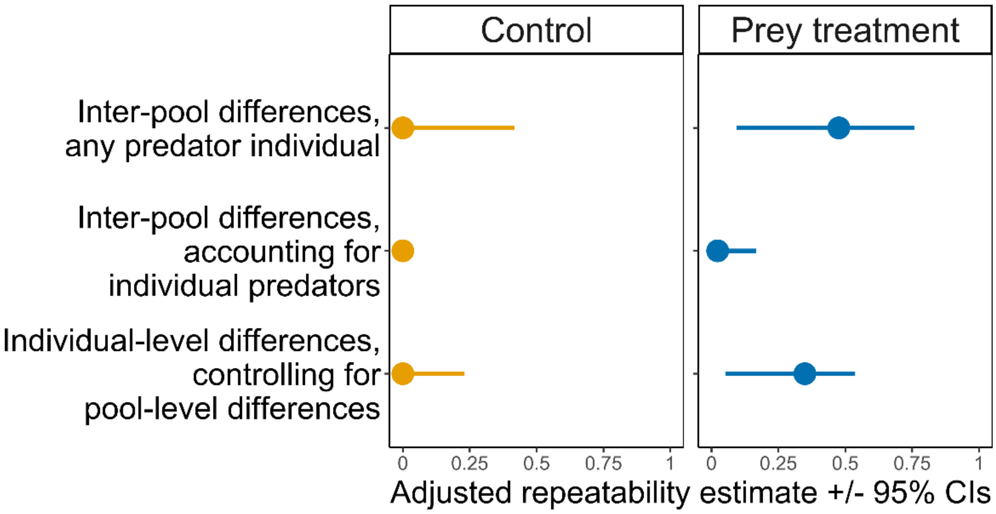


Figure 3.4: Pool- and individual-level repeatability estimates for the time spent near the stimulus, during control (orange) and prey treatment (blue) presentations. The figure shows adjusted repeatability estimates (filled circles), and the degree of uncertainty associated with each estimate (error bars representing 95% confidence intervals). Adjusted repeatabilities represent the proportion of the total variance in the time spent near the stimulus which can be attributed to variation between pools (top and middle rows) or individuals (bottom row), as opposed to variation within pools or individuals. Whereas estimates of inter-pool differences in the upper row are focused on the time spent near the stimulus by any predator individual (pool-level data, **Table 3.1**), those in the middle and lower rows are based on analysis of the time individual predators spent near the stimulus (**Table 3.2**).

3.4.3 Variation between individual predators in their response to prey

To investigate inter-individual variation in predatory behaviour, adjusted repeatabilities were estimated for the time spent near the stimulus by individually-identified pike cichlids. This analysis was limited to pike cichlids which approached the stimulus in at least two separate prey treatment presentations, or in at least two separate control presentations. During prey treatment presentations, the time spent near the stimulus was significantly repeatable between individuals, even when controlling for standard body length and other experimental and environmental variables (R_{ind} = 0.349, 95% confidence interval: 0.053 - 0.537, P = 0.006, N_{obs} = 109, N_{ind} = 44; **Fig. 3.4**, **Table 3.2**). In contrast, repeatable inter-individual differences were not observed in the control treatment (R_{ind} = 0, 95% confidence interval: 0 - 0.231, P = 0.5, N_{obs} = 59, N_{ind} = 24; **Fig. 3.4**, **Table 3.2**). Whilst the time spent near the stimulus was positively correlated across prey treatment presentations, no correlations were evident across control presentations (**Fig. 3.5**). Additionally, with the identity of individual predators factored into these analyses, there was no longer any substantial inter-pool variation in the time spent near the stimulus (R_{pool} = 0.023, 95% confidence interval: 0 - 0.167, P = 0.448, N_{obs} = 109, N_{pool} = 15; **Table 3.2**). This suggests that the inter-pool differences resulted from variation in the behaviour of individual predators in separate pools, rather than other sources of inter-pool variation such as predator density or environmental factors.

Table 3.2: Adjusted repeatability estimates indicating the extent of consistent inter-individual (R_{ind}) and inter-pool (R_{pool}) differences in the time spent near the stimulus, in both control and prey treatment presentations. N_{obs}, N_{ind} and N_{pool} respectively indicate the number of observations, individuals and pools included in these analyses. Adjusted repeatability estimates were similar regardless of whether presentation number (rows 1-2, table below) or the proportion of previous prey treatment presentations (rows 3-4, table below) were included as fixed effects (separate GLMMs were constructed to avoid problems associated with collinearity between these two variables; Zuur, Ieno and Elphick, 2010).

Variables controlled for	**Stimulus treatment**	N_{obs}	N_{ind}	R_{ind}	***P***	N_{pool}	R_{pool}	***P***
time of day, presentation number, no. of pike cichlids in each pool, canopy openness, standard body length	Control	59	24	0 [0, 0.231]	0.500	12	0 [0, 0.069]	0.500
	Prey treatment	109	44	0.349 [0.053, 0.537]	0.006	15	0.023 [0, 0.167]	0.448
time of day, proportion of previous prey treatment presentations, no. of pike cichlids in each pool, canopy openness, standard body length	Control	59	24	0 [0, 0.219]	0.500	12	0 [0, 0.010]	0.500
	Prey treatment	109	44	0.322 [0.050, 0.519]	0.007	15	0.049 [0, 0.190]	0.374

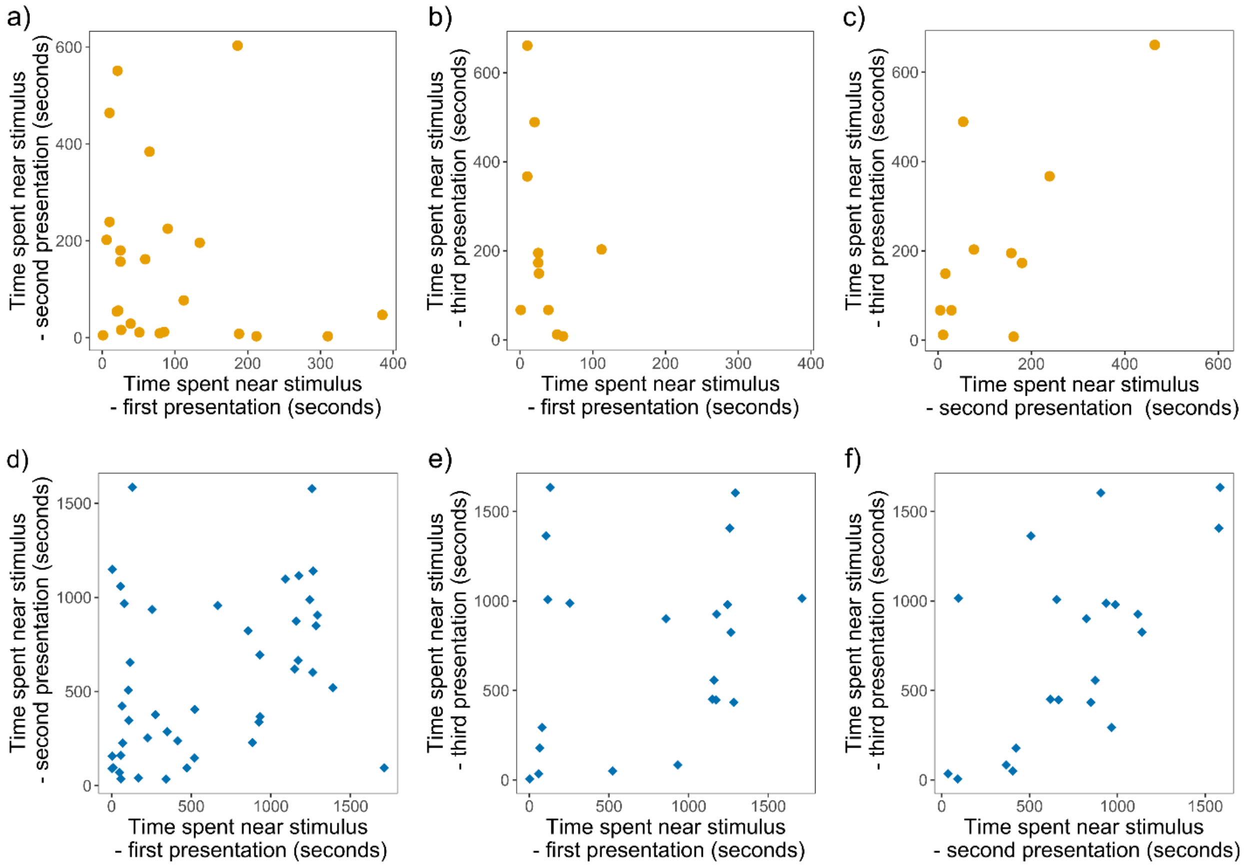


Figure 3.5: Correlations between the time spent near the stimulus during different presentations. Plots show comparisons between different control presentations ([a]-[c], orange dots) and prey treatment presentations ([d]-[f], blue diamonds). Shown are the first versus second presentations in which a pike cichlid was observed (a, d), first and third presentations (b, e), and the second and third presentations (c, f).

3.4.4 Possible effects of sampling bias and social interactions on inter-individual variation in predatory behaviour

Attempts to measure behaviour in natural populations are susceptible to bias because individuals vary in their tendency to engage with novel stimuli (Stuber *et al*., 2013), and because behavioural differences between individuals can be influenced by social interactions (Webster and Ward, 2011; McDonald *et al*., 2006; Bevan *et al*., 2018). In this study, there was a positive association between the number of prey treatment presentations in which an individual approached the stimulus and the time it spent near the stimulus during the first prey presentation it was observed in (Poisson GLMM, $N_{\text{obs}} = N_{\text{ind}} = 68$: $\chi^2_1 = 10.983$, $P < 0.001$; **Fig. 3.6**; Appendix, Supplementary Table 2, model 7). This implies that pike cichlids that approached the stimulus in multiple presentations were more predatory on average, relative to the overall predator population. The individual-level repeatabilities presented here (**Fig. 3.4**) may therefore under-estimate the true extent of inter-individual variation as they are likely to exclude the least predatory individuals. Randomisation simulations based on an approach developed by Ioannou, Ramnarine and Torney (2017) also suggested that variation in the response of pike cichlids to prey was not dependent on the identity of the other individual pike cichlids present within the same pool (**Fig. 3.7a**). Additionally, there was no evidence for positive or negative interactions between predators within the same pool (**Fig. 3.7b**), suggesting that the observed inter-individual differences in predators' response to prey were not magnified or suppressed as a result of social interactions.

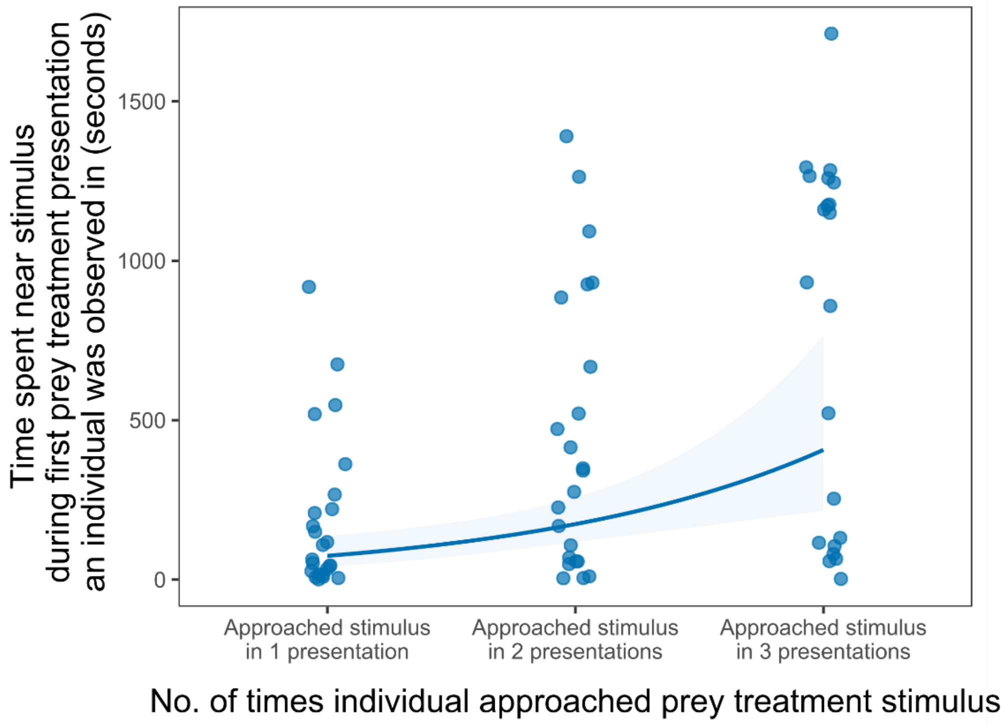


Figure 3.6: Relationship between the number of prey treatment presentations in which individual pike cichlids approached the stimulus and the time spent near the stimulus during the first presentation that an individual was observed in. The curve represents the predicted response derived from a Poisson GLMM (Appendix, Supplementary Table 2, model 7) and the shading represents uncertainty (95% confidence intervals) surrounding this response. Data points are also offset laterally to increase visibility.

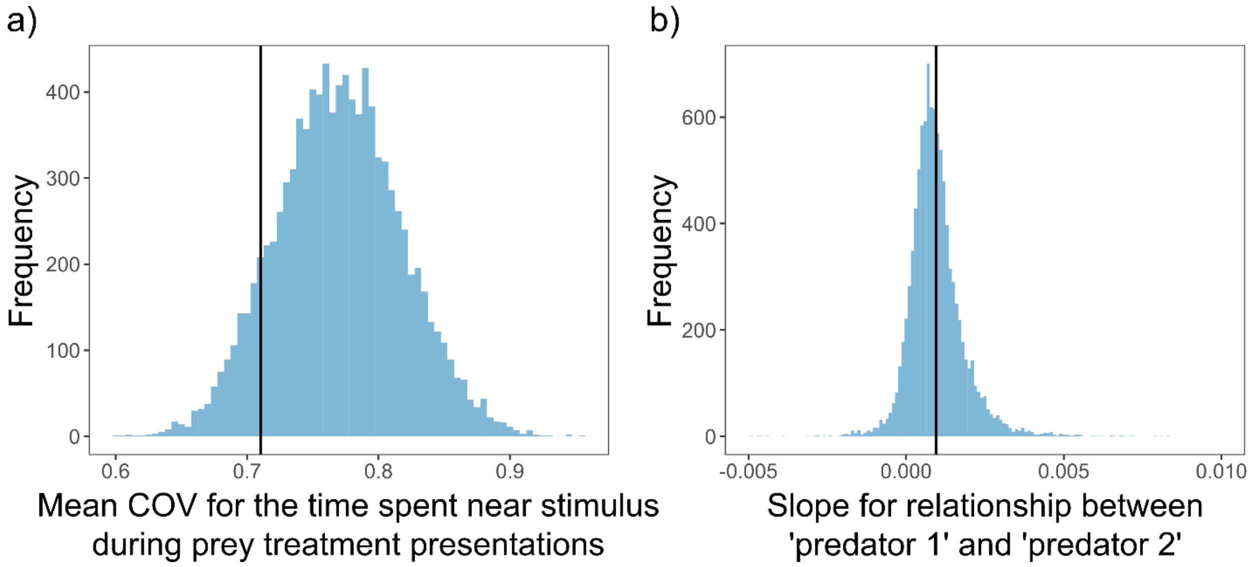


Figure 3.7: Results from randomisation simulations designed to examine the influence of social interactions on inter-individual variation in predators' response to prey, based on 44 individual predators which approached the prey treatment stimulus in multiple presentations. (a) The observed mean group-level diversity (COV) in predators' responses to prey (0.710, indicated by the black vertical line) occurred within the 95% confidence intervals of the randomised distribution for the same statistic, produced when observations corresponding to individual predators were randomly shuffled between pools. (b) The mean slope for the relationship between the time spent near the stimulus by pairs of fish randomly selected from the same pool was weakly positive (mean slope: 0.000976, shown by the black vertical line), but the 95% confidence intervals (-0.000431, 0.00299) of the randomised distribution of the slope overlapped with zero.

3.4.5 Predicting individual predatory responses from behaviour when prey are absent

The comparison of treatments with and without prey shows that the behaviour of individual predators is only repeatable when prey are present. This suggests that the response to prey cannot be explained by personality variation in boldness or neophobia, as consistent differences arising from these traits should also lead to repeatability in the control presentations without prey. To test this explicitly, the next stage of the analysis addressed whether the behaviour of pike cichlids during control treatment presentations could account for the repeatability in their response during prey treatment presentations. Adjusted repeatability estimates in the time spent near the stimulus during the prey treatment remained significantly repeatable when the mean time spent near the stimulus during control presentations was included as a covariate ($N_{\text{obs}} = 109$, $N_{\text{ind}} = 44$: $R_{\text{ind}} = 0.33$, 95% confidence interval: 0.013 - 0.506, $P = 0.003$). The repeatability estimate was still statistically significant when the time spent near the stimulus during the first control presentation an individual was observed in was instead included as a covariate ($N_{\text{obs}} = 109$, $N_{\text{ind}} = 44$: $R_{\text{ind}} = 0.294$, 95% confidence interval: 0.021 - 0.508, $P = 0.006$; in both analyses, individuals were assigned zero time spent near the stimulus in the control if they were not observed in the control treatments).

These results are consistent with the absence of any correlations between the time spent near the stimulus during prey treatment presentations and the mean time spent near the stimulus across control presentations (Poisson GLMM, $N_{\text{obs}} = 87$, $N_{\text{ind}} = 35$: $\chi^2_1 = 0.426$, $P = 0.514$; **Fig. 3.8a**; Appendix, Supplementary Table 2, model 8). There was additionally no correlation between the time spent near the stimulus when prey were present and the time spent near the stimulus during the first control presentation in which an individual pike cichlid was observed (Poisson GLMM, $N_{\text{obs}} = 87$, $N_{\text{ind}} = 35$: $\chi^2_1 = 0.0695$, $P = 0.792$; **Fig. 3.8b**; Appendix, Supplementary Table 2, model 9). There was however a near-significant tendency for individuals observed in control presentations to spend more time near the prey treatment stimulus than those individuals which were never observed in the control (Poisson GLMM, $N_{\text{obs}} = 109$, $N_{\text{ind}} = 44$: $\chi^2_1 = 3.17$, $P = 0.0749$; **Fig. 3.9a**; Appendix, Supplementary Table 2, model 10), providing some indication of a role of boldness in determining the response of individual predators to their prey. In contrast, there was no evidence for an effect of neophobia on the response to prey. Individual pike cichlids which were observed in the first control presentation did not differ in the time spent near the stimulus during the prey treatment from those individuals which were not observed in the initial presentation (Poisson GLMM, $N_{\text{obs}} = 109$, $N_{\text{ind}} = 44$: $\chi^2_1 = 1.14$, $P = 0.285$; **Fig. 3.9b**; Appendix, Supplementary Table 2, model 11).

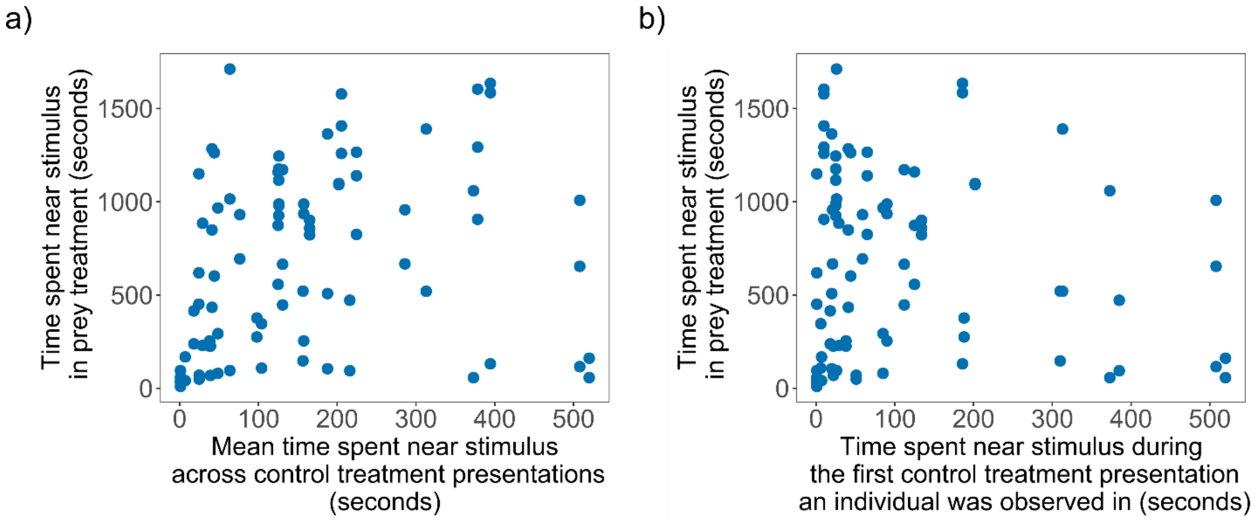


Figure 3.8: The relationship between the time spent near the stimulus during control presentations without prey and the time near the prey treatment stimulus. The time spent near the stimulus by individual predators in separate prey treatment presentations is plotted against the mean time spent near the stimulus across all three control presentations per pool (a), and the time spent near the stimulus during the first control presentation in which an individual was observed (b).

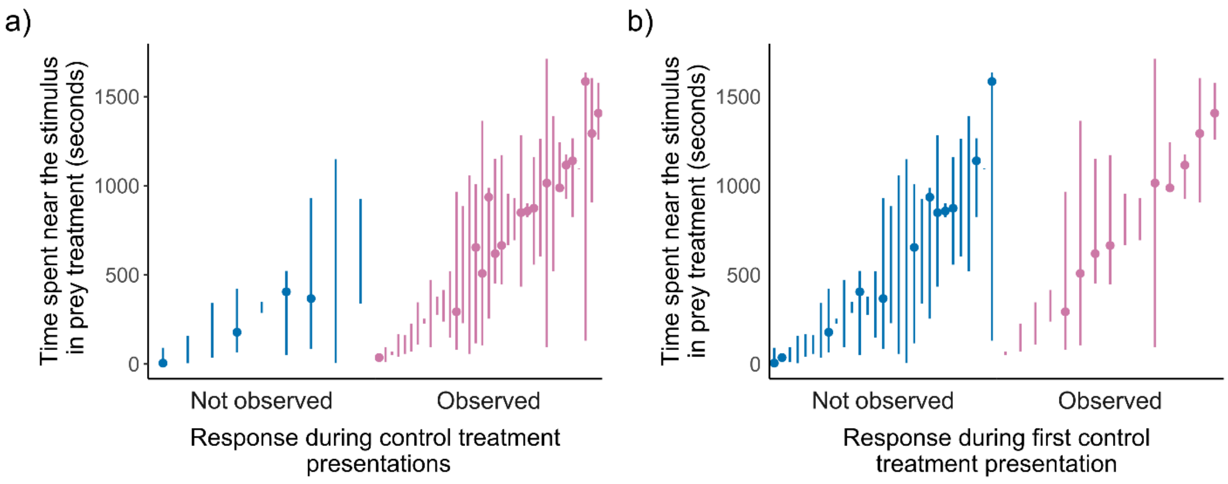


Figure 3.9: The relationship between whether or not individual predators were observed in any of the control presentations without prey (a), or in the first control presentation (b), and the time spent near the stimulus during prey treatment presentations when prey were present. In cases where individuals approached the stimulus in two prey treatment presentations, the vertical lines represent the maximum and minimum amount of time an individual spent near the stimulus in the

two separate presentations. In cases where individuals approached the stimulus in three separate prey treatment presentations, the dots indicate the median value for the time spent near the stimulus.

3.4.6 Components of repeatability in predatory behaviour

One explanation for the increased repeatability of behaviour in the prey treatment compared to the control is that variation between individuals is greater in the presence of prey. To examine this possibility, inter-individual variances for the time spent near the stimulus during the control and prey treatments were estimated. Unlike the adjusted repeatability, these estimates are not influenced by the consistency of individual behaviour (i.e. intra-individual variation) within each treatment. In contrast to negligible inter-individual variability among fish observed across control presentations (N_{obs} = 59, N_{ind} = 24, inter-individual variance: 0, 95% confidence interval: 0 - 0.353), inter-individual variability was apparent in the prey treatment (N_{obs} = 109, N_{ind} = 44, inter-individual variance: 0.597, 95% confidence interval: 0.064 - 0.977; **Fig. 3.10**). The residual variance was also higher in the control (1.645, 95% confidence interval: 0.844 - 2.118) compared to the prey treatment (1.074, 95% confidence interval: 0.713 - 1.49), suggesting that intra-individual variation was lower when prey were present. Thus, the significant repeatability between individuals in the prey treatment and the lack of repeatability in the control can be explained by individuals being more variable relative to one another and also behaving more consistently in the prey treatment.

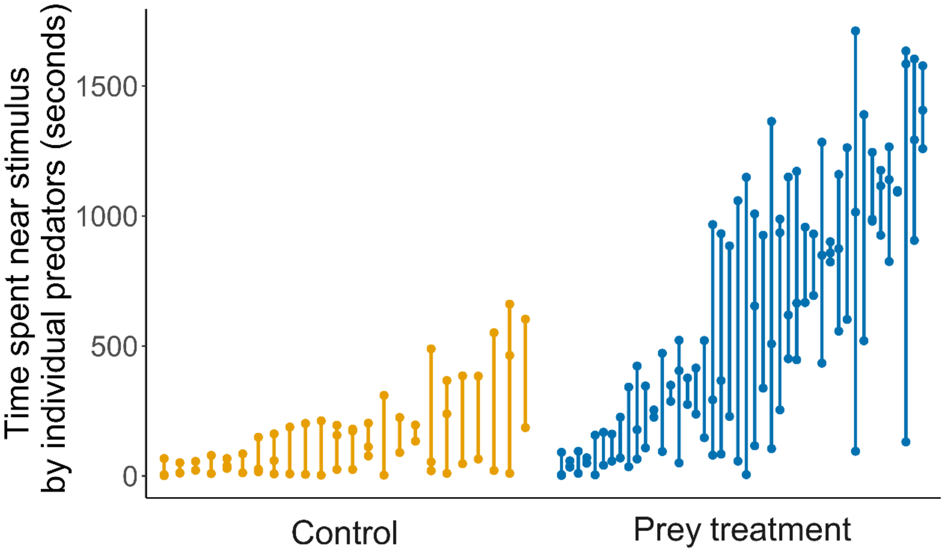


Figure 3.10: Variability in the behaviour of individual predators in the control (orange) and prey treatments (blue). Points indicate the time spent near the stimulus in each presentation, and the vertical lines span the range for each individual. Data is shown for individuals which approached the stimulus in two or more prey treatment presentations (N_{ind} = 44) or two or more control presentations (N_{ind} = 24), ordered by increasing mean time spent near the stimulus.

3.5 Discussion

By examining the response of wild piscivorous fish to a stimulus prey shoal across a series of natural river pools, this study provides evidence for consistent inter-individual variation in the response of predators to their prey. After controlling for their body size and for experimental and environmental factors, individual pike cichlids differed consistently in the time spent near the stimulus when prey were present, but not when prey were absent. Crucially, inter-individual variation in predatory behaviour could not be explained by the response of predators to the empty presentation apparatus (a novel object). This indicates that the response to prey reflects a personality trait which is specific to predation, is distinct from other commonly measured personality traits such as boldness or neophobia, and is independent of the previously documented correlation between boldness, predator activity levels and encounter rates with prey (Ioannou, Payne and Krause, 2008; Pruitt, Stachowicz and Sih, 2012). This individual-level trait accounted for variation between pools in the time spent near the stimulus by any pike cichlid, suggesting that it is likely to explain a significant proportion of the risk faced by prey in their local environment, even when accounting for predator density. This analysis also shows that inter-individual differences in the response to prey were unlikely to have arisen from pre-existing variation between predators becoming magnified due to the presence of prey, as boldness (as measured during control presentations) did not predict individual predators' response to prey. While this study had clear limitations, including the fact that it was impossible to fully standardise test conditions in the wild or account for the potential impact of unmeasured sources of variance (e.g. sex differences) on inter-individual differences in predatory behaviour, this field-based approach did allow predatory responses to prey to be measured in the wild under relatively realistic conditions.

The existence of a personality trait specific to predation could affect prey in two main ways: by influencing the strength of non-lethal effects on prey traits, or by directly affecting prey survival during predator-prey encounters. Most obviously, the sustained or repeated presence of a nearby predator is likely to affect the level of risk perceived by prey, potentially triggering a change in prey behaviour, such as an increase in vigilance, aggregation in larger social groups, or a shift from one microhabitat to another (Lima and Dill, 1990). In this study, the time spent near the stimulus by pike cichlids was also positively correlated with the initial rate at which prey were attacked (during the first 30 seconds spent near the stimulus). This is important because the behavioural response of prey to predation risk will depend on their perception of the impending threat, which will be sensitive to how predators in the vicinity are behaving (Stankowich and Blumstein, 2005). Frequent, repeated attacks on prey are likely to be perceived as a greater threat by prey than the presence of a nearby but non-threatening predator. For prey, a predation-specific personality trait should also make the level of background predation risk perceived by prey more predictable, particularly in situations where the same predator and prey individuals encounter one another frequently, as is the case in relatively isolated pools within the guppy-pike cichlid system.

A predation-specific personality trait could also have a strong influence on the eventual outcome of encounters with prey and help to maintain behavioural variation within prey populations (McGhee, Pintor and Bell, 2013). While this study was not designed to explore the possible direct effects of predator personality on prey survival, these results suggest that inter-individual variation in the predatory behaviour measured here may have potentially lethal consequences for prey. Although there was a positive association between the time spent near the stimulus and the overall probability of attack by pike cichlids, this association might be expected if the number of predatory strikes simply grows linearly with time. However, the positive relationship between the time spent by predators near the stimulus and the initial rate of attack (during the first 30 seconds spent near the stimulus) also implies that predators which spend more time around prey are more motivated to attack when prey are first encountered. These individuals may thus pose a greater threat to prey, but direct, independent measurements of predation rates would be required to fully resolve the impact of inter-individual variation in predatory behaviour on prey survival, and account for the possibility that higher attack rates do not necessarily translate into increased prey mortality rates. Quantifying how individual pike cichlids respond to potential alternative prey types would also shed light on any possible links between predatory personality and individual specialisation in diet in this species (Toscano *et al*., 2016). Having established that individual predators consistently differ in their response to a standardised prey stimulus independently of boldness, future research could also investigate the impact of these differences on dynamic interactions between predators and prey, in a setting where prey are unconstrained and both predators and prey are free to respond to cues from one another. This would address whether prey adjust their anti-predator behaviour in response to predation-specific personality variation. If carried out in a setting where prey were exposed to individual predators for an extended period, this could also help clarify the relative impact on prey survival of a predation-specific personality trait compared to variation between individual predators in commonly studied personality traits which affect encounter rates, such as boldness or activity.

There was also evidence to suggest that consistent inter-individual variation in the behaviour of the predator individuals present within each pool accounted for differences between pools in the time spent near the stimulus by any pike cichlid. Pool-level differences were not correlated with the densities of predators in each pool, suggesting that the personality traits of resident predators could be an important factor contributing to local differences in predation risk. However, in addition to predator density, pools might also differ in the social environment predators are exposed to. If the presence of an individual near the stimulus alerts others to the presence of prey through social information (Pitcher, Magurran and Winfield, 1982), inter-individual differences might be suppressed by social interactions. Alternatively, if socially dominant predators aggressively exclude subordinates from accessing prey, feedbacks resulting from differences in social dominance could also magnify inter-individual variation in the response to prey (Bergmüller and Taborsky, 2010). It was therefore important to account for the possibility that variation between pools in the nature and strength of social interactions could generate the observed inter-individual differences in predator behaviour (Bevan *et al*., 2018). In this study, randomisation simulations showed that the degree of inter-individual variation in the time spent near prey was not dependent on the observed distribution of individual pike cichlids between pools. Although the sociality or aggressiveness of the individual pike cichlids was not measured directly, making it difficult to assess the relationship between these commonly studied personality traits and inter-individual differences in predatory behaviour, the results of the randomisation simulations suggested that there were no social interactions between individual predators that positively or negatively affected inter-individual variation. In other words, being present within a particular pool, and exposed to a particular set of other individuals with specific behavioural characteristics, did not have a strong influence on an individual predator's response to prey. While it is difficult to fully disentangle intrinsic inter-individual differences from environmental influences on behaviour without translocating animals and quantifying their behaviour in different contexts (Niemelä and Dingemanse, 2017), these findings support the conclusion that stable differences in social interactions were unlikely to have played a major role in shaping the observed inter-individual variation in the response to prey.

By demonstrating that the risk prey are likely to experience cannot always be adequately predicted from frequently studied axes of personality variation, this study highlights the importance of considering inter-individual variation in traits with direct ecological relevance. These results also have specific implications for the guppy-pike cichlid system, in which geographically isolated guppy populations occupying low- and high-predation environments demonstrate dramatic differences in numerous aspects of their life history (Reznick, Bryga and Endler, 1990) and behaviour (Ioannou, Ramnarine and Torney, 2017). Since high-predation zones are characterised by the presence of pike cichlids, the existence of differences in predator behaviour between pools adds to the accumulating evidence that predation pressure is more heterogeneous within these areas than implied by the well-studied contrast between high- and low-predation environments (Barbosa *et al.*, 2018; Deacon, Jones and Magurran, 2018). Finally, by revealing how individual predators consistently differ in their response to prey, these findings also underscore the value of studying the behaviour of predators in their natural environment, after the point when prey have been encountered.

Chapter 4:

Differential anti-predator responses of prey to inter-individual variation in predator behaviour

One of the pike cichlids (*Crenicichla frenata*)
included in the study presented in Chapter 4.
Photograph: A. W. Szopa-Comley.

4.1 Abstract

The capacity to adjust anti-predator behaviour flexibly represents a key adaptation for prey animals exposed to fluctuating levels of predation risk. Empirical studies suggest that prey assess current levels of risk using a variety of cues, ranging from broad indicators of a predator's presence to subtle changes in the behaviour of nearby predators, and match the intensity of their anti-predator response to the severity of the immediate threat. Despite accumulating evidence that individual predators often vary repeatably in the level of threat they represent, and indications that these differences are linked to personality traits such as boldness, it remains unclear whether prey respond differentially to predators with contrasting behavioural types. To explore the relationship between predator personality and prey anti-predator responses, shoals of guppies (*Poecilia reticulata*) were exposed to visual contact with their pike cichlid (*Crenicichla frenata*) predators in artificially constructed experimental pools. The behaviour of individual pike cichlids was repeatedly measured both with and without prey in order to quantify inter-individual variation in boldness (the time taken to leave a refuge when prey were absent) and in the response of predators to prey. Pike cichlids showed consistent inter-individual variation in boldness, but during trials with prey, the only behaviour that was repeatable over multiple days was the proportion of time individual predators spent near prey. The activity of the guppy shoals was higher when exposed to predators which spent a greater proportion of their time near prey, indicating that prey were sensitive to an aspect of predator behaviour which differed repeatably between individual pike cichlids. Increased shoal cohesion was associated with reduced levels of predator refuge use and more frequent attacks, but there was no strong evidence for consistent inter-individual differences in these predator behavioural traits across multiple days. Despite these plastic prey responses, the boldness of individual predators when tested alone was a poor predictor of prey behaviour. These results emphasise the acute sensitivity of prey to the behaviour of nearby predators, but also caution against assuming that predator boldness levels will accurately predict how prey respond to their predators.

4.2 Introduction

The need to avoid predation is an inescapable feature of life for most animals, which must be continually balanced with other vital activities, such as foraging, territory defence and reproduction (Lima and Dill, 1990). While prey survival can be enhanced by anti-predator responses such as heightened vigilance, reduced activity and shifts to safer habitats, these tactics often come at the cost of reducing the time available for foraging (Lima, 1998), resulting in lower energy intake, and negative impacts on components of prey fitness (Sheriff, Krebs and Boostra, 2009; Christianson and Creel, 2010; Clinchy, Sheriff and Zanette, 2013). Joining larger and more cohesive groups also offers powerful protection from predators by reducing an individual's *per capita* risk, as a result of the dilution (Foster and Treherne, 1981), attack abatement (Turner and Pitcher, 1986), collective vigilance (Martín, Luque-Larena and López, 2006) and confusion effects (Ioannou *et al*., 2008). The decision to join larger and more cohesive groups can also be costly, since it has the potential to strengthen competition over resources (Krause and Ruxton, 2002; Hoare *et al*., 2004; Ward, Webster and Hart, 2006) and increase the probability of acquiring contact-spread parasites (Stephenson *et al*., 2015). The threat posed by predators can vary dramatically between microhabitats and over time, but the costs of responding with superfluous or inappropriately intense anti-predator behaviour are often high (Lima and Dill, 1990). According to the threat-sensitivity hypothesis, it should therefore benefit prey to be acutely sensitive to the factors predicting current levels of predation risk (Helfman, 1989; Brown *et al*., 2006), including the behaviour of nearby predators (Stankowich and Blumstein, 2005).

There is extensive evidence which indicates that prey rely on information from both coarse-grained predator cues and fine-scale variation in predator behaviour to evaluate the current threat posed by predators, and adjust their anti-predator behaviour in response to the perceived threat level. When exposed to different predator species, prey modify their anti-predator response depending on the severity or the type of threat the predator represents (Curio, Klump and Regelmann, 1983; Krupa and Sih, 1998; Owings *et al*., 2001; Stapley, 2004; Templeton and Shriner, 2004; Botham *et al*., 2006, 2008). As well as responding to the presence or absence of particular predator species, the strength of anti-predator responses often varies with the intensity of specific cues, such as the concentration of predator odour compounds (Kusch, Mirza and Chivers, 2004; Ferrari, Kapitania-Kwok and Chivers, 2006). Similarly, prey adjust their anti-predator behaviour in response to variation in visual cues which provide accurate information on the magnitude or location of the immediate threat, such as the predator's body size (Bishop and Brown, 1992; Puttlitz *et al*., 1999; Chivers *et al*., 2001; Engström-Öst and Lehtiniemi, 2004), shape (Magurran and Girling, 1986; Rieucau *et al*., 2014), proximity (Curio and Regelmann, 1985; Stankowich and Goss, 2005; Catano *et al*., 2016) and approach speed (Stankowich and Blumstein, 2005). Studies examining how predators and prey interact over the course of an encounter also demonstrate that prey are sensitive to fine-scale variation in predator behaviour. As predators transition from an initial non-threatening state to approaching within close proximity and finally attacking prey, prey typically respond to the escalating threat level by ratcheting up their anti-predator response (Magurran and Pitcher, 1987; Nøttestad *et al*., 2002; Ratcliffe *et al*., 2011; Corcoran, Wagner and Conner, 2013; Storms *et al*., 2019; Romenskyy *et al*., 2019). Observations of predator inspection behaviour also indicate that prey modify their anti-predator behaviour after approaching within close range of a predator (Pitcher, Green and Magurran, 1986), suggesting that behavioural cues may be important in revealing how motivated the predator is to attack (Csányi, 1985; Murphy and Pitcher, 1997; Smith and Belk, 2001). Further studies have additionally shown that prey attune their anti-predator behaviour to subtle variation in the predator's posture, orientation and activity state (Helfman, 1989; Kent *et al*., 2019). Although the available evidence suggests that monitoring both the coarse-grained and fine-scale behavioural cues of predators is crucial in enabling prey to assess current levels of predation risk, relatively little is known about how prey respond to the consistent behavioural differences between individual predators which are commonly observed in predator populations (Araújo, Bolnick and Layman, 2011; Sih *et al*., 2012).

Consistent differences between individual predators in widely measured traits such as activity, boldness, aggressiveness and exploration can be an important factor influencing prey survival (Exnerová *et al*., 2010; Pruitt, Stachowicz and Sih, 2012; Toscano and Griffen, 2014; Chang *et al*., 2017; Michalko and Řežucha, 2018). Research exploring the consequences of animal personality variation has shown that more active, bolder and more exploratory individuals tend to move through their environment at a higher rate and switch between foraging locations more rapidly (van Overveld and Matthysen, 2010; Patrick, Pinaud and Weimerskirch, 2017; Schirmer *et al*., 2019), affecting encounter rates with prey. Compared to their shy counterparts, bolder predators are also more tolerant of risk from their own predators and consequently spend more time actively hunting in less safe habitats (Ioannou, Payne and Krause, 2008; Dammhahn and Almeling, 2012). The link between fast-slow life history differences and behavioural variation within predator populations provides further support for this relationship: individuals with fast life histories sustain rapid growth through energy gains brought about by actively foraging in risky habitats (Réale *et al*., 2007; Nakayama, Rapp and Arlinghaus, 2016). Prey exposed to bold predators are therefore likely to experience more frequent and persistent predation cues. As reported in Chapter 3, individual predators also differ in their behavioural response to prey, raising the possibility that predators with contrasting behavioural types vary in how they interact with prey, with potential consequences for the prey's perception of risk. One of the few studies to examine how inter-individual variation in predatory behaviour influences prey anti-predator responses showed that individual pike predators (*Esox lucius*) differed repeatably in how rapidly they orient towards lone three-spined stickleback (*Gasterosteus aculeatus*) prey (McGhee, Pintor and Bell, 2013). The speed with which pike oriented towards prey was found to determine the duration of the stickleback's anti-predator freezing response, which in turn influenced the time taken for the pike to launch an attack. Although this study did not directly test whether inter-individual differences in orientation or attack speed were associated with commonly studied personality traits, bolder or more active predators are expected to evoke a heightened anti-predator response. Alternatively, there may be little difference in how prey respond to individual predators from opposite ends of the behavioural spectrum, particularly if the individuals within a population all pose a substantial risk to prey regardless of their behavioural type. Due to overwhelming costs of being killed by a predator, and the ensuing tendency of prey to overestimate predation risk (Bouskila and Blumstein, 1992), further information on the predator's personality might be of little additional value to prey (Stephens, 1989; Luttbeg *et al*., 2020).

Predators and prey coexist within close proximity of one another in many natural environments, including freshwater aquatic habitats and coral reefs, where visual cues are particularly important in allowing prey to assess current levels of predation risk (Pitcher, 1980; Leahy *et al*., 2011). These conditions are commonly found in high-predation populations of Trinidadian guppies (*Poecilia reticulata*), which are regularly confined to the same relatively isolated river pools as their pike cichlid (*Crenicichla frenata*) predators when water levels recede during the dry season (Magurran, 2005; Botham *et al*., 2006). Compared to Trinidadian guppies from populations which are not exposed to predators such as the pike cichlid, guppies from high-predation habitats typically exhibit heightened anti-predator responses, including increased shoal cohesion (Botham *et al*., 2008; Herbert-Read *et al*., 2017a), which functions to reduce predation risk through a variety of mechanisms (Krause and Ruxton, 2002). Guppies from high-predation habitats also routinely modify their behaviour after inspecting a predator, suggesting that they are likely to benefit from gaining more accurate information about the behaviour of predators in their immediate vicinity (Dugatkin and Godin, 1992).

By exposing shoals of high-predation guppies (*Poecilia reticulata*) to visual contact with wild-caught pike cichlid (*Crenicichla frenata*) predators in artificial experimental pools (**Fig. 4.1a**), I investigated whether the strength of prey anti-predator responses was correlated with inter-individual variation in predator behaviour. Within each experimental pool, predators had access to multiple refuges, resembling the conditions found in natural river pools where predators intermittently emerge from cover to approach and attack prey (Botham *et al*., 2005). Groups of guppies were held within glass tanks located in the centre of each experimental pool, allowing visual contact between the predator and the prey, but also preventing prey from being captured. This experimental set-up allowed the behaviour of the predator and prey to be recorded simultaneously, and also enabled the refuge use of individual predators to be repeatedly measured in contexts both with and without prey. As refuge use is associated with boldness, this provides a direct link between the natural behaviour of pike cichlids and a widely assayed personality trait reflecting the tendency of individuals to prioritise foraging gains over risk avoidance (Wilson *et al.*, 2011; Balaban-Feld *et al.*, 2019a). When predators and prey were both present within the experimental pool, guppies were expected to show a heightened anti-predator response when exposed to pike cichlids with a greater tendency to leave the refuge. During these trials, the behaviour of predators and prey was measured at two points in time: after predators and prey had been in visual contact for a short period (30 minutes), and after a longer period (4-7 hours). This provided an opportunity to test whether the strength of the prey anti-predator response was reinforced or declined with increasing exposure.

4.3 Methods

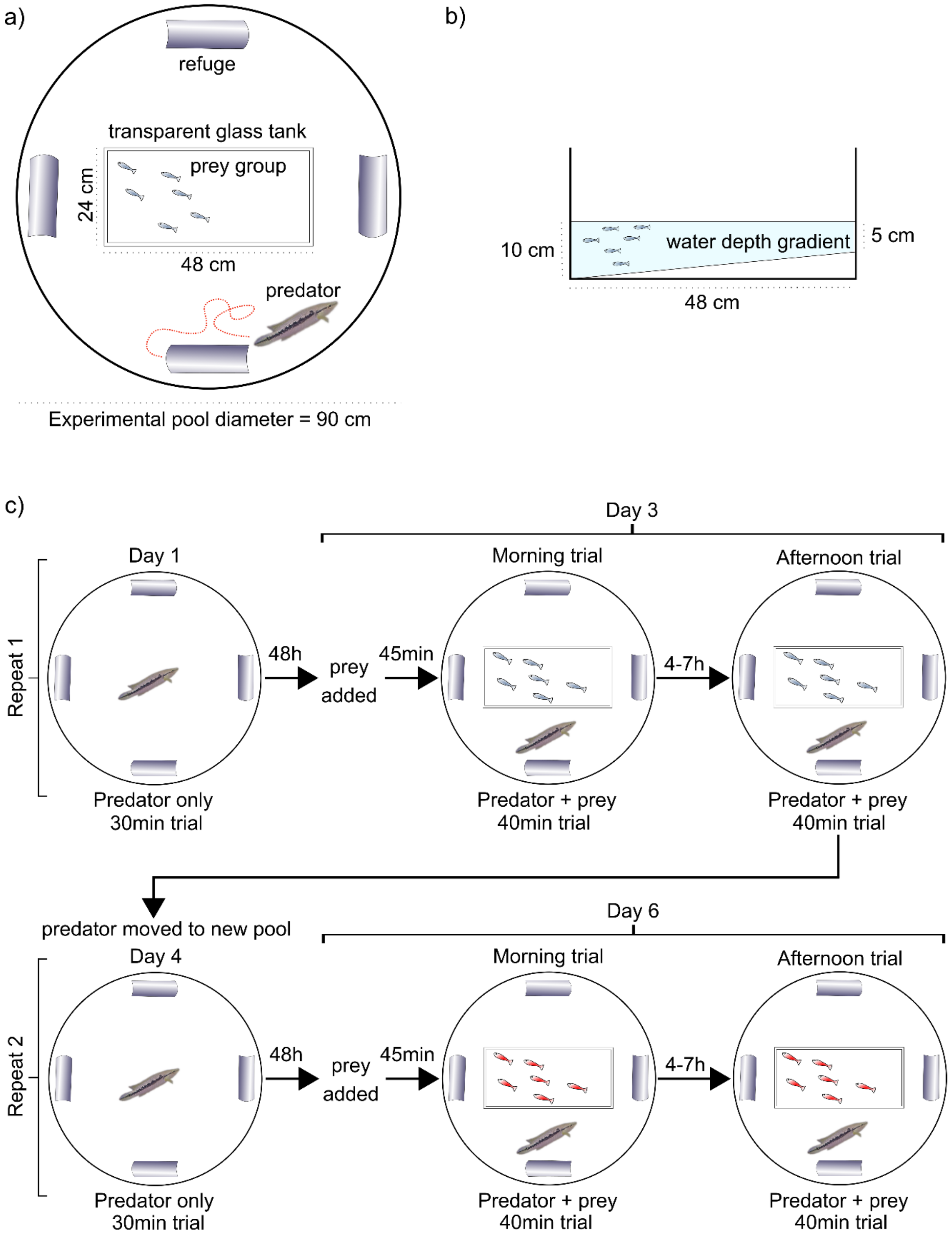
4.3.1 Subjects

Pike cichlids (39 individuals; mean standard body length (SBL): 9.7 cm, standard deviation: 2.6 cm) were caught on multiple days in late March and throughout April 2018 from two sites in the Caura (Tacarigua) river in Trinidad (site latitude/longitude: 10^{o}41.5187’ N/61^{o}21.4927’ W; 10^{o}42.3108’ N/61^{o}21.4440’ W). Pike cichlids were caught using funnel traps or with a baited rod and line. Two different capture methods were used to reduce bias in the sample of caught individuals towards a particular behavioural type (Wilson *et al.*, 2011). Guppies used in the experiment were caught from a non-sympatric population in the Lopinot valley (site coordinates: 10^{o}41.0031’ N, 61^{o}19.5569’ W), as fish from this population were likely to display a strong anti-predator response due to the presence of pike cichlids (Botham *et al.*, 2008), but would not have previously encountered the individual predators used in the study. Prior to being tested, pike cichlids and guppies were kept in separate outdoor holding pools (diameter = 120 cm, depth = 90 cm), in the same location as the experimental pools. The time interval between the date when pike cichlids were caught and the first day of testing varied from 4 to 11 days. Once the experiment had been completed, the pike cichlids used in the experiment were returned to the wild at the same collection sites.

4.3.2 Experimental pools

Experimental pools were constructed within an enclosed garden at the University of the West Indies campus in Trinidad, and consisted of an inner circular pool (Chad Valley three-ring paddling pool; internal diameter = 90 cm, depth = 30 cm), placed within a larger outer circular tub (internal diameter = 120 cm, depth = 90cm). The inner pool had a white lining, inflatable green walls and was filled with aged water to a depth of 10 cm. During the experiment, pike cichlids were released into the inner pool, which contained four cylindrical refuges made from opaque PVC piping (diameter = 8 cm, length = 20 cm). The shoal of six female guppies was held within a rectangular glass tank (dimensions: length = 48 cm, width = 24 cm, height = 28 cm), placed in the centre of each experimental pool. This design allowed visual contact between predator and prey but prevented the guppies from being captured (**Fig. 4.1a**). The glass tank was fitted with a sloping floor made from white opaque plastic, in order to create a water depth gradient along the longitudinal axis of each tank ranging from a minimum depth of 5 cm to a maximum of 10 cm (**Fig. 4.1b**). In order to minimise disturbance from the external environment, the outer circular tub was covered by a detachable white polyester sheet, overlaid on top of a shallow pyramidal scaffold constructed from four 75 cm lengths of PVC piping.

During trials without prey, experimental pools were filmed from above using a GoPro Session video camera secured to a tripod. During trials with prey, an additional camcorder (Panasonic SD 800) was also suspended from the same tripod to obtain a higher resolution recording of the prey group in the glass tank. In all trials, both video cameras were positioned over the centre of the inner pool (approximately 1 m above the inner pool). At the start of each trial, the cameras were moved into place by inserting the tripod arm underneath the covering to minimise disturbance. Within the garden enclosure, experimental pools were positioned 2 metres apart from one another under dappled shade, to minimise changes in temperature over the course of a day. Six different pools were constructed and remained in the same position throughout the experiment.



<u>Figure 4.1:</u> Artificial pools used in the experiment and overview of the experimental procedure. (a) View of the experimental pool from above. (b) Side view of the centrally positioned central glass tank. (c) Schematic overview of the procedure for each pike cichlid. Individuals were tested in the same sequence of behavioural trials in repeat 1 (days 1-3) and 2 (days 4-6), albeit after being transferred to a different experimental pool. On day 3 and 6, the guppy shoal was added to the central glass tank 45 minutes before the start of the morning trial (during the first 15 minutes of this period, the predator and the prey were not in visual contact). A previously untested guppy shoal was used in each repeat. All diagrams in panels (a-c) are not to scale.

4.3.3 Experimental procedure

Six individual pike cichlids were tested concurrently in each run of the experiment, which lasted 6 days. During a run of the experiment (**Fig. 4.1c**), the sequence of behavioural trials from day 1 to 3 (repeat 1) was repeated on day 4 to 6 (repeat 2) for each individual pike cichlid. On day 1, the behaviour of the pike cichlid was filmed for 30 minutes directly following their release into one of the experimental pools, in order to provide a measure of personality variation (specifically boldness, i.e. the time taken to leave the refuge) in a context without prey. Before the start of each trial, individual pike cichlids were caught from their holding pools by trapping the fish within a cylindrical refuge. Fish were then moved directly to an experimental pool by gently transferring the refuge containing the predator to a position close to the edge of the inner pool. Prior to release of the predator into the pool, three additional refuges were also arranged around the pool edge, and once the predator had been released, the cover of the pool was secured in place immediately afterwards. This approach was chosen instead of netting the fish and releasing them directly into the centre of the pool because it was less likely to induce stress. Trials started once the pool covering had been secured in place. After the trial was over, an empty glass tank subsequently used for the guppy shoal was placed in the centre of each experimental pool. At this point in the experiment, the sides of the glass tank were covered with white sheets of plastic.

Pike cichlids were then left to habituate to their new surroundings for 24 hours, at which point the refuge use of the predator was recorded again on day 2 for a 40-minute period. On day 3 (**Fig. 4.1c**), a group of 6 female guppies was introduced into the glass tank in the centre of each experimental pool. The groups of guppies were haphazardly netted from the prey holding pool. After a 15-minute habituation period, the white plastic covering the sides of the tank was removed, allowing visual contact between predator and prey for the first time. Interactions between pike cichlids and the guppy shoal were subsequently recorded in two predator-prey trials: 30 minutes (morning trials) and 4 - 7 hours (afternoon trials) after the point when visual contact between the prey and the predator was first possible. Predator-prey trials lasted 40 minutes, and started when the white sheets covering the experimental pool were moved back into position. Immediately before the start of each trial, 300ml of water was transferred from the predator's side of the pool into the glass tank, and *vice versa*, to ensure olfactory cues were available to both predators and prey.

As only two experimental pools could be filmed simultaneously, predator-prey trials were conducted in a staggered fashion, with trials beginning at one of three recording times. The order in which trials were filmed was determined by randomly allocating individual predators to one of the three recording times. Due to the need to maintain a consistent time gap between the morning and afternoon predator-prey trials on the same day, the same trial order was maintained in both the morning and afternoon. Morning trials took place between 0650 and 1230, and afternoon trials between 1320 and 1730.

On day 4 (**Fig. 4.1c**), pike cichlids were moved to a different experimental pool, which was assigned at random. Experimental pools were drained and re-filled with aged water prior to these moves. On days 4-6, pike cichlids were subjected to the same sequence of behavioural trials (repeating days 1-3). On day 6, trial order was also randomised, with the proviso that the recording time was not the same in both repeats. On day 6, groups of guppies were formed from untested individuals which had not previously been exposed to a predator on day 3, with the result that pike cichlids encountered prey groups composed of different individuals on day 3 and day 6. On each day of the experiment, predators were fed two mealworms after trials had been conducted. The water temperature remained between 24°C and 26.5°C throughout the experiment. The standard body length (SBL) of individual pike cichlids was measured once at the end of the experiment.

In summary, the experimental procedure resulted in two measures of refuge use without prey per individual predator (day 1 and day 4), and four measures of predator behaviour during trials with prey, including two trials on day 3 and two on day 6 (see **Fig. 4.1c**). Within predator-prey trials conducted on the same day, repeated measures of predator behaviour were split between those which took place after predators and prey were exposed to each other for 30 minutes (morning predator-prey trials) and those which took place after 4 - 7 hours (afternoon predator-prey trials). In total, 39 individual pike cichlids were tested, resulting in a total sample size of 78 trials without prey and 156 predator-prey trials. However, due to intermittent problems with the video cameras in outdoor conditions, complete data on predator behaviour were only available for 154 trials, and on the prey response for 140 trials.

4.3.4 Video analysis

Measures of predator behaviour were obtained from videos manually using BORIS event-logging software (version 7.8.2; Friard and Gamba, 2016). Videos were analysed blind to the identity of the individual predator. In trials without prey on days 1 and 4, the time taken for individual pike cichlids to first leave the refuge was extracted from videos as a measure of boldness, since the latency to leave a refuge tends to be associated with the propensity to engage in other risky activities (Wilson *et al.*, 2011; Hulthén *et al.*, 2016) and is known to correlate with foraging gains and susceptibility to predation in other species of fish (McDonald *et al.*, 2016; Balaban-Feld *et al.*, 2019a). In all trials both without and with prey, predators were considered to have left a refuge when the full extent of the predator's body was outside of the cylindrical refuge tube. In trials with prey, the time spent outside of a refuge was defined as the total amount of the time during a trial when the predator had fully emerged. The time spent near prey was defined as the total amount of time in each trial that at least half the predator’s body was within a zone extending 10 cm in all directions around the central rectangular tank containing the group of guppies. Attacks on prey were defined as fast directed movements towards the prey shoal.

Coordinates corresponding to the position of each guppy within the central tank were extracted manually from video recordings using a custom python script (utilising python version 3.6.9, and OpenCV version 4.1.1) once videos had been converted to AVI format using FFmpeg video processing software (version 4.4.2). The positions of guppies were extracted at 10-second intervals, beginning from the start of the trial to the end of the trial. Due to slight differences between trials in the height of the camera above the experimental arena, the coordinates obtained from videos were scaled from pixels to centimetres based on an object of known length.

In each trial, five variables describing the behaviour of the prey group were then calculated: i) the mean distance of individual guppies to the group centroid, ii) the mean nearest neighbour distance for guppies within the group, iii) the distance moved by the group centroid between each 10 second interval, iv) the distance between the group centroid and the deep end of the glass tank (corresponding to the distance along the 5 cm depth gradient within the tank) and v) the length-width ratio of the minimal bounding box encompassing the prey group. The mean value of each variable over the course of a trial was then used in subsequent analyses. Distance to the group centroid and nearest-neighbour distances are both frequently used to quantify group cohesion (Herbert-Read *et al*., 2017a). Distance moved by the group centroid should reflect the activity of the guppy shoal (Ginnaw *et al*., 2020). The distance between the group centroid and the deep end of the tank was measured as guppies may respond to heightened perceived risk by moving into shallower areas, since predation risk is known to increase with water depth for this prey species (Mattingly and Butler, 1994; Croft *et al*., 2006). The length-width ratio of the minimal area bounding box encompassing the prey group should reflect the extent to which the guppy shoal forms an elongated (high length to width ratio) or relatively compact (low length to width ratio) shape (Hemelrijk and Hildenbrandt, 2008).

4.3.5 Statistical analysis

All statistical analyses were carried out in R version 3.5.1 (R Development Core Team, 2019). Consistent inter-individual variation in predator behaviour was quantified by using generalised linear mixed effects models (GLMMs) to estimate adjusted repeatabilities. Adjusted repeatabilities in this context are defined as:

$$Adjusted\ repeatability, R = \frac{\sigma_i^2}{\sigma_i^2 + \sigma_\varepsilon^2}$$

where σ_i^2 indicates the variance explained by individual i and σ_ε^2 refers to the residual variance (Nakagawa, Johnson and Schielzeth, 2017). Here, the adjusted repeatability estimate conveys the amount of behavioural variation which can be attributed to individuals, as a proportion of the total phenotypic variance, excluding the variance explained by other potentially confounding variables fitted as fixed effects or other random intercept terms included within the model (Nakagawa and Schielzeth, 2010). GLMMs were either fitted directly using the lme4 package (for negative binomial GLMMs; version 1.1-21), or analysed using the rptR package (for Poisson and binomial GLMMs; version 0.9.22; Stoffel, Nakagawa and Schielzeth, 2017). Whereas for Poisson GLMMs, σ_ε^2 can be calculated by adding the distribution-specific variance to the variance explained by an additive over-dispersion term (i.e. the excess variation compared to the expected variation under a Poisson distribution, estimated by the model), these components cannot be readily isolated in negative binomial GLMMs and σ_ε^2 can only be approximated (Nakagawa, Johnson and Schielzeth, 2017). For negative binomial GLMMs, σ_ε^2 was therefore estimated using the trigamma function, following the method outlined by Nakagawa, Johnson and Schielzeth (2017).

For trials on day 1 and day 4 in which prey were absent (**Fig. 4.1c**), inter-individual differences in the time taken for pike cichlids to first leave the refuge were analysed with a Poisson GLMM. The model was fitted to data on the subset of individuals for which repeated measures were available (i.e. the 21 individuals which left the refuge in the trial conducted on day 1, as well as those on day 4). This model included repeat number (repeat 1 corresponds to day 1, repeat 2 corresponds to day 4, see **Fig. 4.1c**), trial order (i.e. the first, second or third recording time within a day) and the standard body length (SBL) of the individual pike cichlid as fixed effects, in order to account for the influence of these variables on the inter-individual differences in predator behaviour.

For trials on day 3 and day 6 in which prey were present (**Fig. 4.1c**), adjusted repeatability estimates were first obtained by including both the morning and afternoon predator-prey trials in the same analysis. Binomial GLMMs were first used to quantify consistent inter-individual variation in whether or not pike cichlids left a refuge at all during a trial (predator emergence), using all available data from 154 trials. Individual-level repeatabilities for the total amount of time spent by predators outside of a refuge, the proportion of this time spent near prey, the number of attacks on prey and the rate of attack (number of attacks per minute spent outside the refuge) were also estimated, using data on individual pike cichlids which repeatedly emerged from the refuge (23 individuals, observations from 70 trials). These data were analysed by fitting negative binomial, binomial, Poisson and negative binomial GLMMs, respectively. All GLMMs included repeat number (repeat 1 corresponds to day 3, repeat 2 corresponds to day 6, see **Fig. 4.1c**), predator-prey trial (i.e. morning or afternoon), trial order (i.e. the first, second or third recording time within a day) and SBL as fixed effects. As previous research indicates that pike cichlids are more active around midday (Endler, 1987), the predator-prey trial x trial order interaction was also included as a fixed effect in all models to account for the possibility that the effect of trial order was dependent on whether trials were conducted in the morning or in the afternoon. This interaction term allowed the effect of trial order to vary between morning and afternoon trials, thus capturing the expected effect of time of day on predator behaviour. All GLMMs included crossed random intercepts for both individual ID and experimental pool ID (included to account for any consistent effects of the pool on predator behaviour).

For the variables describing predator behaviour when prey were present, the same analyses were also performed separately for data only from the morning or only from the afternoon predator-prey trials (see **Fig. 4.1c**). Since personality variation is defined as consistent inter-individual differences in behaviour which are stable over time, analysing data from the morning and afternoon trials separately was necessary in order to confirm that inter-individual differences in predator behaviour were maintained across different days, without inflating adjusted repeatability estimates by including trials from within the same day. While adjusted repeatability estimates obtained from the larger combined data-set are likely to be more precise, estimates based on data split between the morning and afternoon predator-prey trials are less likely to reflect short-term differences in hunger or motivation, which is predicted to result in greater consistency in behaviour within the same day. GLMMs used to analyse the split data included the same fixed effects and random intercepts as those used in the analysis described above, but did not include the predator-prey trial x trial order interaction, or the main effect of predator-prey trial.

Throughout the analysis of repeatability, the statistical significance of the adjusted repeatability estimates was evaluated by: i) determining whether the 95% confidence intervals surrounding each estimate, obtained via parametric bootstrapping, included zero, and ii) using likelihood ratio tests to compare a model with the relevant random intercept to a model lacking this term. All instances in which fish failed to leave the refuge were disregarded from the analysis, rather than replacing these observations with a maximum value corresponding to the length of a trial (for the time taken to first leave the refuge) or zeroes (for the time spent outside of a refuge). This was done to avoid influencing adjusted repeatabilities by biasing estimates of intra-individual variation (Stamps, Briffa and Biro, 2012).

Additional GLMMs were constructed to examine whether the behavioural response of the pike cichlids differed between the morning or afternoon predator-prey trials (see **Fig. 4.1c**). Models were fitted to data on five separate behavioural responses: predator emergence (i.e. whether or not the pike cichlid left a refuge at all during a trial), the time spent outside of a refuge, the proportion of time spent near prey, the number of attacks and the rate of attack. For each response variable a model comparison approach was used to compare the relative fit of several competing models: a baseline model featuring just repeat (i.e. repeat 1 or 2, see **Fig. 4.1c**), trial order (i.e. the first, second or third recording time within a day) and SBL as explanatory variables; an otherwise identical model which also included predator-prey trial (i.e. morning or afternoon) as an additional explanatory variable; and a model including both predator-prey trial and the interaction between predator-prey trial and trial order (identical to the models used to estimate individual-level adjusted repeatabilities). Within a comparison set, the relative fit of the models within each set was assessed using model AICc (Akaike's Information Criterion corrected for small sample sizes) values, which balance how closely a model fits the data with the overall complexity of the model. AICc differences of greater than two units were taken to indicate strong support for one model over another (Burnham and Anderson, 2002). The relative fit of a model including the main effect of predator-prey trial (i.e. morning or afternoon) was compared with that of the baseline model to provide an indication of the influence of this variable on different aspects of predator behaviour.

The relationship (inter-individual correlation) between the boldness of individual predators during trials without prey and the behaviour of the same individuals when prey were present was assessed by fitting a bivariate mixed effects model, using the MCMCglmm package in R (version 2.29; Hadfield, 2010). Since raw phenotypic correlations between mean values of repeatedly assayed behavioural traits do not always correspond to correlations at the inter-individual level (Brommer, 2013; Niemelä and Dingemanse, 2018), analyses capable of partitioning behavioural variation into differences between and within individuals are regarded as more robust methods for determining whether the responses of individual animals are correlated across behavioural traits (Dingemanse and Dochtermann, 2013; Houslay and Wilson, 2017; Moiron, Laskowski and Niemelä, 2020). As the time taken to leave a refuge during trials without prey and the proportion of time spent near prey were shown to differ consistently between individuals at an earlier stage of the analysis, only the inter-individual correlation between these two traits was estimated. The analysis was restricted to data on individual pike cichlids which repeatedly left the refuge during trials without prey and which also repeatedly emerged from the refuge during the trials with prey (95 observations of 19 individual fish). The model used a Poisson distribution for the time taken to first leave the refuge and a binomial distribution for the proportion of time spent near prey, and included the following explanatory variables: repeat number (i.e. 1 or 2, see **Fig. 4.1c**), standard body length, trial order (i.e. the first, second or third recording time within a day), predator-prey trial (i.e. morning or afternoon) and the predator-prey trial x trial order interaction. Explanatory variables were mean centred and scaled to standard deviation units prior to fitting the model. The model also included random intercepts for predator and experimental pool ID, and was configured to fit an unstructured covariance matrix for both random intercepts, indicating that the model was set up to estimate the variance in both response variables, and the covariance between them. As repeated measures for the time taken to first leave the refuge and the proportion of time spent near prey were obtained from different trials, the intra-individual covariance was constrained to equal zero, following the method outlined by Dingemanse and Dochtermann (2013). Since MCMCglmm relies on a Bayesian approach, in which the posterior distribution for model parameters is proportional to the likelihood multiplied by the prior distribution, the model was fitted using flat uninformative inverse Gamma priors, which should have a minimal influence on the results. The model was fitted conservatively with a Markov chain consisting of 2,500,000 iterations, with a burnin of 500,000 (indicating the number of iterations which were discarded at the start of the chain) and a thinning length of 5,000 (indicating the interval between sampled iterations). Model convergence was assessed by checking the degree of auto-correlation between sampled iterations of the Markov chain using the autocorr.diag() function found within MCMCglmm, for both the fixed effects and the variance components estimated by the model. The posterior distribution for the inter-individual correlation estimate was calculated from the model output by dividing the estimated covariance between the two behavioural traits by the product of the square root of the variance associated with the two traits. The mean of this distribution is reported as the inter-individual correlation estimate, and the uncertainty surrounding the correlation estimate was reflected in the reported 95% credible intervals.

Linear and generalised linear mixed-effects models (GLMMs/LMMs) were also used to examine which predator behaviour variables best predicted mean prey responses, averaged over a trial, during trials in which pike cichlids and guppies were in visual contact. Using a similar model comparison approach to the method described above, two sets of competing models including different predator behaviour variables were constructed for each prey response variable analysed. The first model comparison set was designed to test the effect of predator emergence (i.e. whether or not the pike cichlid left the refuge at all during a trial) on the prey response. These models were fitted to data from all predator-prey trials (140 trials). The second model comparison set was constructed to determine whether there were any relationships between predator and prey behaviour within the subset of trials in which pike cichlids did emerge from the refuge (71 trials). Within this set, separate models were fitted including the following predator behaviour variables: the time spent outside of a refuge, the proportion of time spent near prey and the number of attacks on prey during a trial. Both model comparison sets also included an additional model featuring the boldness of individual pike cichlids as an explanatory variable (the mean time taken to leave the refuge during trials without prey, on days 1 and 4). When calculating mean boldness levels, maximum values of 1800 seconds (corresponding to the length of a trial) were used for trials in which the pike cichlid did not leave the refuge.

LMMs fitted with the lme4 package were used to analyse data on the mean distance of prey to the group centroid, the mean nearest neighbour distance, the distance moved by the group centroid between each 10 second interval and the distance between the group centroid and the deep end of the glass tank. Gamma GLMMs (fitted with the glmmTMB package) were used to analyse the length-width ratio of the minimal area bounding box encompassing the prey group. All the models constructed within each set included repeat (i.e. 1 or 2, see **Fig. 4.1c**), predator-prey trial (i.e. morning or afternoon), trial order (i.e. the first, second or third recording time within a day), the trial order x predator-prey trial interaction and SBL as explanatory variables, in order to account for these potentially confounding effects. Within each set of models, a baseline 'null' model including only these fixed effects and without any predator behaviour explanatory variables was also included to serve as a comparison point for the other predator behaviour models. As above, relative differences in model fit were judged on the basis of AICc differences. Additionally, for each predator behaviour variable analysed, another model featuring an interaction between the predator behaviour variable and predator-prey trial (i.e. morning or afternoon) was also added to the set. These models were compared to those including the relevant main effects but lacking the interaction term, in order to test whether the relationship between predator and prey behaviour was dependent on the amount of time predators and prey had been exposed to one another.

Throughout the analyses, all (G)LMMs included individual predator ID and experimental pool ID as random effects. To aid model fitting, all continuous explanatory variables were also mean centred and scaled to standard deviation units. For GLMMs, the DHARMa R package (version 0.2.7) was used to verify that model assumptions were met by visually inspecting plots of scaled residuals vs. fitted values, inspecting QQ-plots highlighting deviations of the scaled model residuals from the expected distribution, and directly testing for overdispersion (Hartig, 2020). Assumptions of LMMs were checked by using QQ-plots to verify that model residuals were normally distributed and plots of residuals vs. fitted values to confirm homogeneity of variance. For both GLMMs and LMMs, QQ-plots were also used to confirm that the conditional means for the model random intercepts were normally distributed (Schielzeth *et al.*, 2020).

4.4 Results

4.4.1 Consistent inter-individual differences in predator behaviour in trials without prey

In trials with no prey, 19 out of 39 pike cichlids left the cover of the refuge and emerged into the open areas of the experimental pool in two separate trials (on both day 1 and day 4 of the experiment). Within the subset of the predators which repeatedly emerged from the refuge, the time taken for individuals to first leave the refuge was strongly repeatable (R = 0.534, 95% confidence intervals: 0.071 - 0.782, P = 0.008).

4.4.2 Consistent inter-individual differences in predator behaviour when prey were present

During trials in which predators and prey were in visual contact (i.e. predator-prey trials), 32 pike cichlids left the starting refuge at least once across a total of 79 out of 154 trials. When data from the morning and afternoon predator-prey trials were combined and analysed together, individual predators differed consistently in whether or not they left the refuge they started the trial in (i.e. predator emergence; **Table 4.1**). In trials in which predators left the starting refuge at least once, both the time individual predators spent outside of a refuge and the proportion of time spent near prey were significantly repeatable (**Table 4.1**). However, predators did not exhibit significant consistent inter-individual differences in either the number of attacks or the rate of attacks on prey (**Table 4.1**). For all variables analysed, there was no consistent variation in predator behaviour between experimental pools (**Table 4.1**), suggesting that the location of an experimental pool had a negligible effect on the pike cichlid behaviour.

<u>Table 4.1:</u> Adjusted repeatability estimates for the behavioural response of individual pike cichlids during predator-prey trials, in which predators and prey were in visual contact. Models used to obtain adjusted repeatability estimates were fitted to data from both morning and afternoon predator-prey trials, and included a maximum of 4 repeated measures per individual predator.

Behavioural response	**Sample size**	**Individual-level adjusted repeatability (95% confidence intervals)**	***P*-value**	**Experimental pool-level adjusted repeatability (95% confidence intervals)**	***P*-value**
Predator emergence (binary variable)	39 individuals, 154 observations	0.306 (0.05 - 0.539)	< 0.001	0 [0 - 0.073]	1
Time spent outside of a refuge	23 individuals, 70 observations	0.548 (0.227 - 0.670)	< 0.001	0 (0 - 0.076)	1
Time spent near prey, as a proportion of the time spent outside of a refuge	23 individuals, 70 observations	0.134 (0.033 - 0.243)	< 0.001	0.038 (0 - 0.1)	0.037
Number of attacks	23 individuals, 70 observations	0.376 (0 - 0.66)	0.016	0 (0 - 0.163)	0.491
Rate of attack (no. of attacks per minute spent outside refuge)	32 individuals, 79 observations	0.120 (0 - 0.256)	0.003	0.003 (0 - 0.998)	0.09

When data from the morning and afternoon predator-prey trials were analysed separately, significant individual-level repeatability was only apparent during the afternoon trial in the amount of time pike cichlids spent near prey (as a proportion of the total time spent outside of a refuge), but not during the morning trial (**Fig. 4.2; Table 4.2**). For both predator emergence and the time spent outside of a refuge, the 95% confidence intervals for the adjusted repeatability estimates included zero, indicating that these behaviours were not significantly repeatable between individual pike cichlids when morning and afternoon trials were considered separately.

Additionally for predator emergence, the individual-level adjusted repeatability estimate obtained when combining data from the morning and afternoon predator-prey trials (*R* = 0.306, **Table 4.1**) was only comparable to the repeatability estimated for afternoon trials (*R* = 0.292, **Table 4.2**), and was markedly higher than the repeatability obtained during for morning trials (*R* = 0.09, **Table 4.2**). In contrast, for the time spent outside of a refuge, only the individual-level repeatability estimates obtained using data from morning predator-prey trials (*R* = 0.551, **Table 4.2**) were similar to the repeatability estimate obtained when analysing data from morning and afternoon predator-prey trials together (*R* = 0.529, **Table 4.1**). Although the difference in the number of observations per individual between the combined and separate analyses made it difficult to draw firm conclusions, the relative lack of repeatability between repeats in predator emergence during morning trials, and in the time spent outside of a refuge during afternoon trials, suggests that inter-individual differences in behaviour were not maintained across days for these variables. The relatively high individual-level repeatability for the time spent outside of a refuge obtained when data from morning and afternoon predator-prey trials were analysed together may therefore have resulted from greater consistency in the behaviour of individuals within the same day, rather than consistency across days.

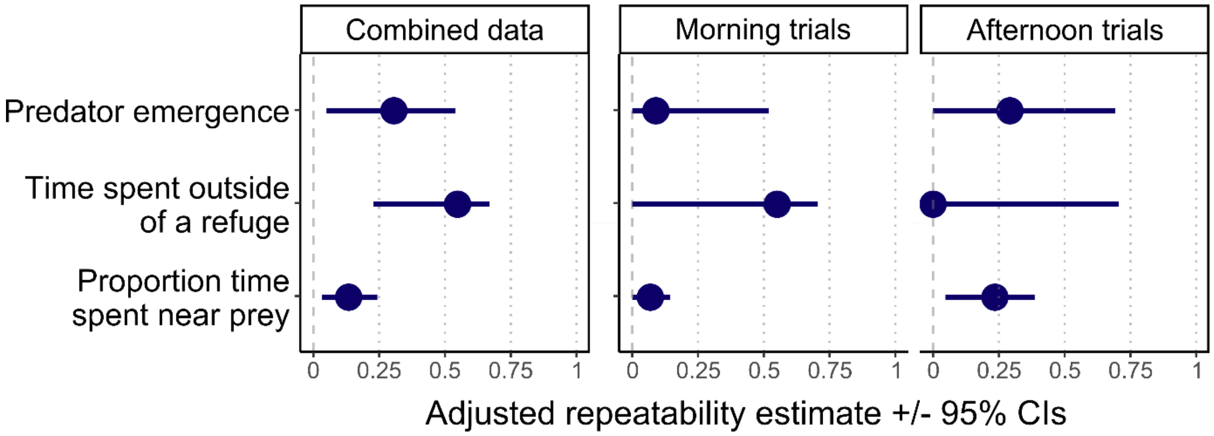


Figure 4.2: Comparison of adjusted repeatabilities for the behavioural response of pike cichlids between estimates obtained when combining data from both morning and afternoon predator-prey trials (left-hand side panel), and estimates obtained when morning and afternoon predator-prey trials were analysed separately (right-hand side panel). Results are shown for predator responses which were significantly repeatable between individuals when analysing the combined data.

Table 4.2: Adjusted repeatability estimates for the behaviour of individual pike cichlids during trials in which predators and prey were in visual contact, considering morning and afternoon predator-prey trials separately. Both subsets of the data included 2 repeated measures per individual.

Behavioural response	**Data subset**	**Sample size**	**Individual-level adjusted repeatability (95% confidence intervals)**	***P*-value**
Predator emergence (binary variable)	Morning	39 individuals, 78 observations	0.09 (0 - 0.518)	0.286
	Afternoon	39 individuals, 76 observations	0.292 (0 - 0.693)	0.062
Time spent outside of a refuge	Morning	14 individuals, 28 observations	0.551 (0 - 0.706)	0.166
	Afternoon	12 individuals, 24 observations	0 (0 - 0.181)	1
Time spent near prey, as a proportion of the time spent outside of a refuge	Morning	14 individuals, 28 observations	0.069 (0 - 0.144)	0.044
	Afternoon	12 individuals, 24 observations	0.235 (0.047 – 0.386)	0.003

4.4.3 Changes in predator behaviour between trials with prey

The mean behavioural response of pike cichlids during predator-prey trials (i.e. trials in which predators and prey were in visual contact) was dependent on the amount of time predators and prey had been exposed to one another. Pike cichlids spent proportionally less time near prey and attacked prey fewer times in the afternoon predator-prey trial, which took place after 4 to 7 hours of exposure, compared to the morning predator-prey trial, which took place 30 minutes after visual contact between the predator and the prey shoal was possible, suggesting the predators acclimatised to the presence of prey (**Fig. 4.3**). For these two response variables, models including predator-prey trial (i.e. morning or afternoon), as well as repeat number, trial order (i.e. the first, second or third recording time within a day) and SBL, received greater support from the data than an otherwise identical model lacking predator-prey trial as an explanatory variable (**Table 4.3**). Models including non-interacting effects of predator-prey trial and trial order also received more support from the data than models featuring the interaction between these two variables, indicating that the influence of predator-prey trial on the proportion of time spent near prey or the number of attacks was not strongly dependent on the start time of a trial. In contrast, there was no effect of predator-prey trial on the probability that pike cichlids left the refuge, the time spent by predators outside of a refuge or the rate of attack, as demonstrated by the fit of models including these explanatory variables compared to baseline models including repeat, trial order and SBL as explanatory variables (**Table 4.3**).

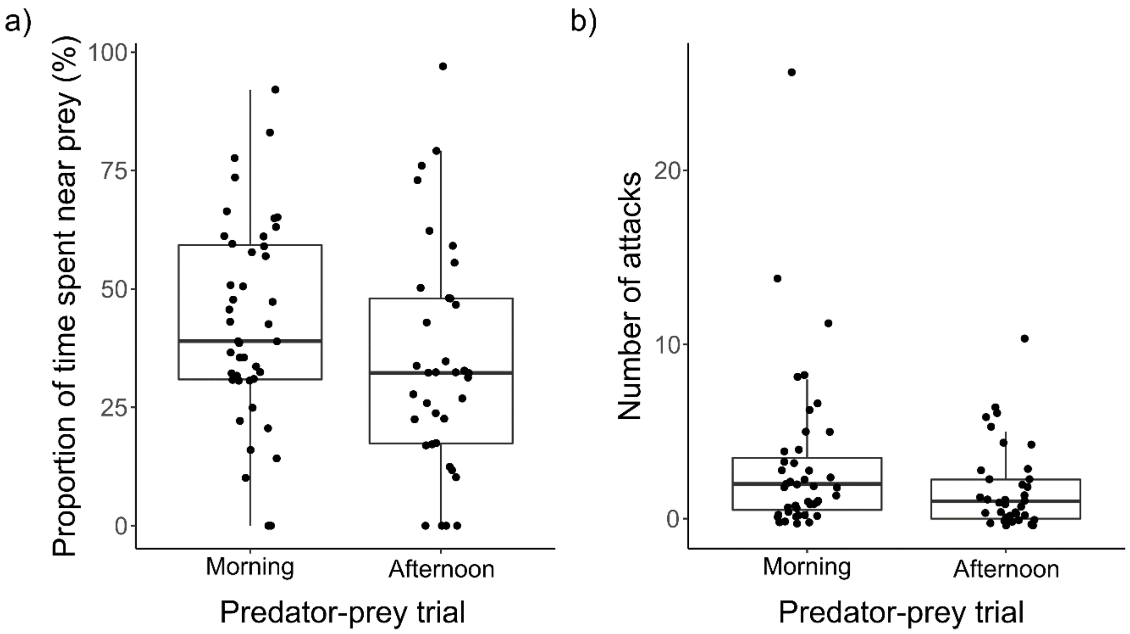


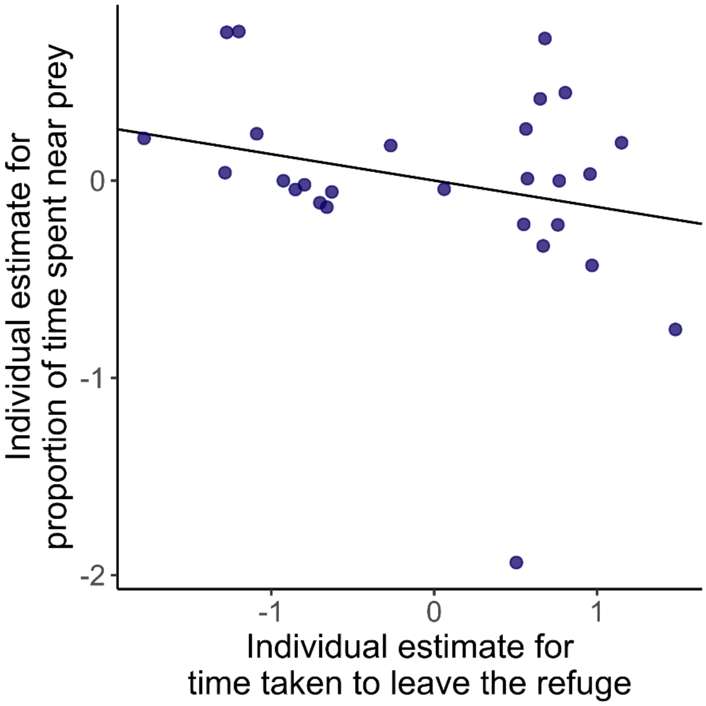
Figure 4.3: Change in predator behaviour between morning and afternoon predator-prey trials, in (a) the time predators spent near prey, as a proportion of the total time spent outside of a refuge, and (b) the number of attacks on prey.

Table 4.3: Results of GLMMs used to examine the influence of the amount of time predators and prey were exposed to one another (the predator-prey trial variable) on predator behaviour. For each response variable describing the behaviour of the predator, model comparisons are between models including predator-prey trial as an explanatory variable and those lacking this variable. All GLMMs included random intercepts for individual ID and experimental pool ID.

Common model structure	**Additional explanatory variable**	**df**	**AICc**	**ΔAICc**
Predator emergence (binary variable) ~ Repeat + Trial order + SBL	None (baseline model)	6	268.0	0.00
	Predator-prey trial	7	269.6	1.67
	Predator-prey trial x Trial order	8	271.5	3.52
Time spent outside of a refuge ~ Repeat + Trial order + SBL	None (baseline model)	7	1163.1	0.00
	Predator-prey trial	8	1164.3	1.20
	Predator-prey trial x Trial order	9	1165.2	2.17
Time spent near prey, as proportion of time spent outside a refuge ~ Repeat + Trial order + SBL	Predator-prey trial	7	2539.6	0.00
	Predator-prey trial x Trial order	8	2541.3	1.63
	None (baseline model)	6	2646.9	107.22
Number of attacks ~ Repeat + Trial order + SBL	Predator-prey trial	7	358.4	0.00
	Predator-prey trial x Trial order	8	360.5	2.13
	None (baseline model)	6	380.8	22.41
Rate of attack (no. of attacks per minute spent outside refuge) ~ Repeat + Trial order + SBL	Predator-prey trial	8	174.7	0.00
	None (baseline model)	7	176.5	1.77
	Predator-prey trial x Trial order	9	176.9	2.23

4.4.4 Inter-individual correlations between predator behaviour with and without prey

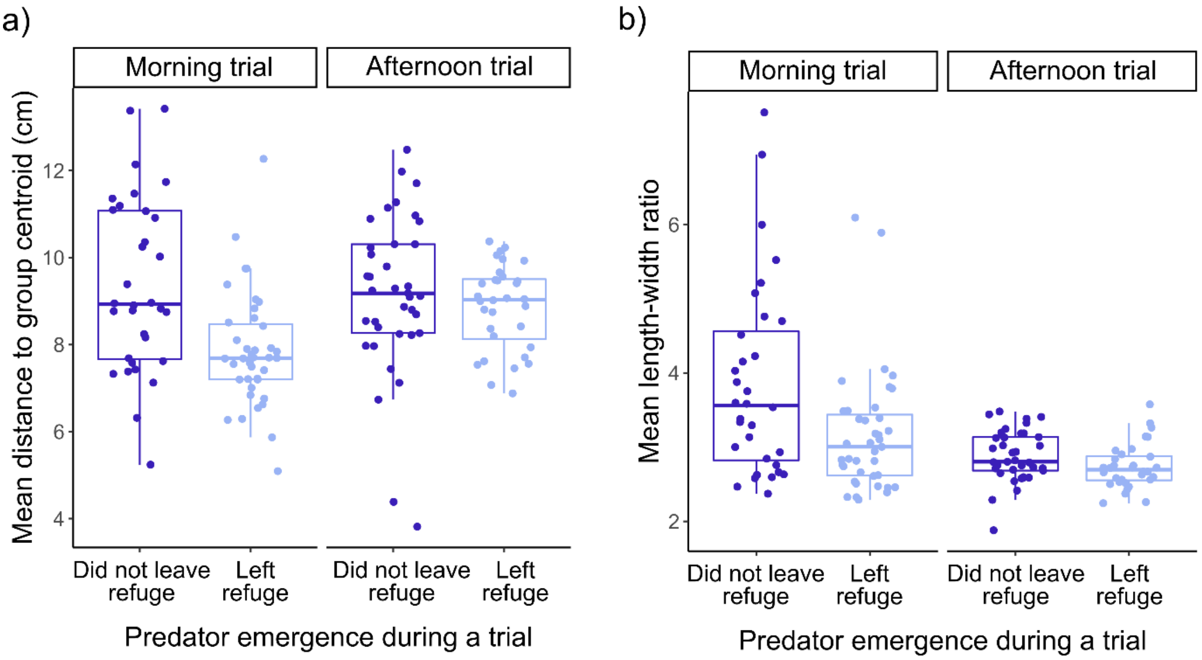
Inter-individual differences in the time taken by predators to first leave the refuge in trials without prey were weakly negatively correlated with inter-individual differences in the proportion of time spent near prey during predator-prey trials (r_{ind} = -0.230, 95% credible intervals: -0.79 - 0.49; **Fig. 4.4**). While this suggests that individual pike cichlids that took longer to leave the refuge (i.e. were less bold) in trials without prey also spent proportionally less time near prey, the wide 95% credible intervals surrounding this estimate, which overlapped with zero, indicate that this relationship was associated with considerable uncertainty, and therefore did not reflect a statistically significant positive association.



<u>Figure 4.4:</u> Inter-individual correlation between the time taken to first leave the refuge during trials without prey and the proportion of time spent near prey (relative to the total amount of time spent outside of a refuge) during predator-prey trials. Data points represent the individual estimates for the two behavioural traits obtained from the bivariate mixed effects model used to determine the strength of the inter-individual correlation.

4.4.5 Relationships between predator and prey behaviour: all trials including prey

The relationship between predator behaviour during trials with prey and the mean distance of guppies to their group's centroid differed between morning and afternoon trials, suggesting that the effect of predator behaviour was dependent on the amount of time predators and prey were exposed to one another. During morning trials, in which predators and prey had been in visual contact for only 30 minutes, the mean distance of prey to the group centroid was reduced when predators left the refuge at least once, compared to trials in which predators never emerged (**Fig. 4.5a**). However, there was no effect of predator emergence during afternoon trials, in which the predator and prey had been exposed to each other for 4 - 7 hours (**Fig. 4.5a**). As evidence of this, the model including an interaction between predator emergence (i.e. whether or not the pike cichlid left the refuge) and predator-prey trial (i.e. morning or afternoon) represented an improvement in fit over the baseline model, whereas the simpler model including non-interacting main effects for predator emergence and predator-prey trial received a similar level of support to the baseline model (**Table 4.4a**). Additionally, compared to the interaction between predator emergence and predator-prey trial, the boldness of individual predators (as determined in trials without prey) had a weaker influence on the mean distance to the group centroid (**Table 4.4a**).



<u>Figure 4.5:</u> Relationships between predator emergence during a trial and the mean distance of individual prey to their group's centroid (a), and the mean length-width ratio of the minimal bounding box encompassing the prey group (b). Relationships are shown for both morning and afternoon predator-prey trials.

In contrast to the associations between predator behaviour and the mean distance to the prey group centroid, there was no influence of predator emergence on the mean nearest neighbour distances within the prey group (**Table 4.4b**). However, during morning predator-prey trials, the mean length-width ratio of the minimal bounding box encompassing the prey group was lower when pike cichlids left the refuge compared to trials in which pike cichlids did not leave, indicating that the shape of the prey group was less elongated during trials in which the predator emerged (**Fig. 4.5b**). During afternoon trials, the mean length-width ratio of the prey group was lower overall compared to the morning trials, and there was no effect of predator emergence (**Fig. 4.5b**). The statistically important effect of the interaction between predator emergence and predator-prey trial was confirmed in model comparisons (**Table 4.4c**): a model including an interaction between predator emergence and predator-prey trial (i.e. morning or afternoon) represented a substantial improvement in fit over the baseline model (**Table 5.4c**). There was also moderate support for the interaction model over the simpler model which only included these variables as main effects (**Table 4.4c**). Additionally, there was no evidence for an effect of the boldness of individual predators, as quantified during trials without prey, on either mean nearest neighbour distances or the elongation of the prey shoal (**Table 4.4b-c**).

Table 4.4: Results from models explaining variance in the mean distance of individual guppies to the prey group centroid (a), the mean nearest neighbour distance (b) and the minimal bounding box encompassing the prey group (c), over the course of a trial. LMMs were used for (a) and (b), whereas the results presented in (c) are from Gamma GLMMs.

	Common model structure	**Additional predator behaviour explanatory variable**	**df**	**AICc**	**ΔAICc**
a)	Mean distance to the group centroid ~ Repeat + Predator-prey trial x Trial order + SBL	Predator emergence x Predator-prey trial	11	518.7	0.00
		Predator emergence (binary variable)	10	520.3	1.55
		Boldness (in trials without prey)	10	520.7	1.98
		None (baseline model)	9	521.4	2.72
		Boldness (in trials without prey) x Predator-prey trial	11	523.0	4.29
b)	Mean nearest neighbour distance ~ Repeat + Predator-prey trial x Trial order + SBL	None (baseline model)	9	375.3	0.00
		Predator emergence (binary variable)	10	379.1	3.82
		Boldness (in trials without prey)	10	380.4	5.19
		Predator emergence (binary variable) x Predator-prey trial	11	381.2	5.99
		Boldness (in trials without prey) x Predator-prey trial	11	384.2	8.92
c)	Mean length-width ratio of minimal bounding box encompassing prey group ~ Repeat + Predator-prey trial x Trial order + SBL	Predator emergence (binary variable) x Predator-prey trial	11	288.3	0.00
		Predator emergence (binary variable)	10	290.2	1.91
		None (baseline model)	9	292.8	4.55
		Boldness (in trials without prey) x Predator-prey trial	11	293.3	5.04
		Boldness (in trials without prey)	10	294.2	5.96

There were no associations between the mean distance moved by the prey group centroid every 10 seconds and whether or not predators left the refuge or the boldness of individual predators in trials without prey. Models including these explanatory variables did not represent a substantial improvement in fit over the baseline model (**Table 4.5a**). However, the mean position of prey groups shifted towards the shallower end of the tank (i.e. the mean distance between the prey group centroid and the deep end of the tank increased) during trials in which predators emerged from the refuge, with some indication that this effect emerged or strengthened during afternoon trials (**Fig. 4.6**). In support of this, the model including the interaction between predator emergence (i.e. whether or not the predator left the refuge) and predator-prey trial received most support from the data, and represented a substantial improvement over the baseline model (**Table 4.5b**). There was also moderately strong evidence to suggest that the interaction model performed better than the model featuring only main effects for predator emergence and predator-prey trial (**Table 4.5b**). Additionally, there was no indication (**Table 4.5b**) that the mean distance moved by the prey group or the position of the group centroid along the water depth gradient was influenced by the boldness of individual predators (as determined separately in trials without prey).

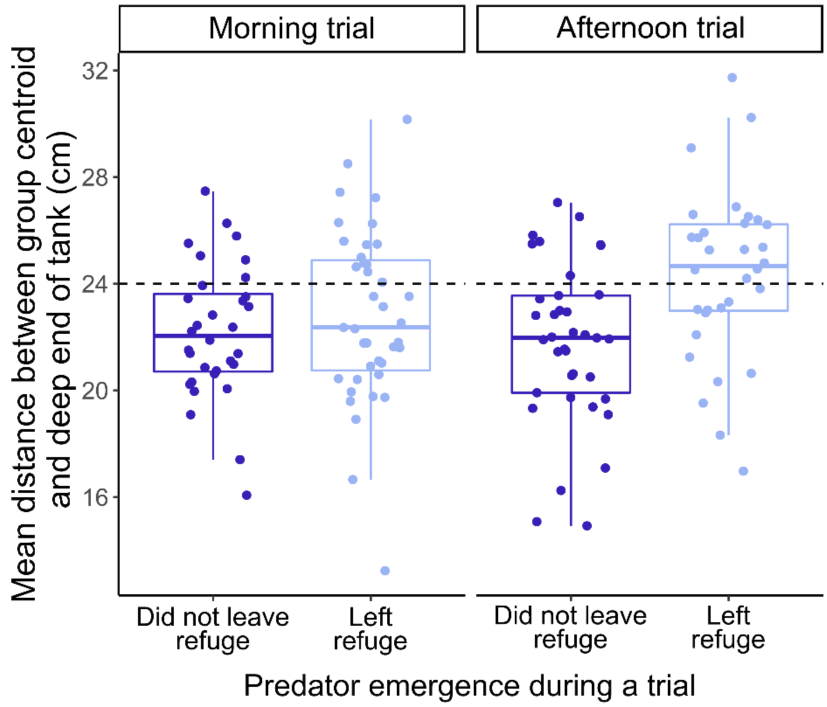


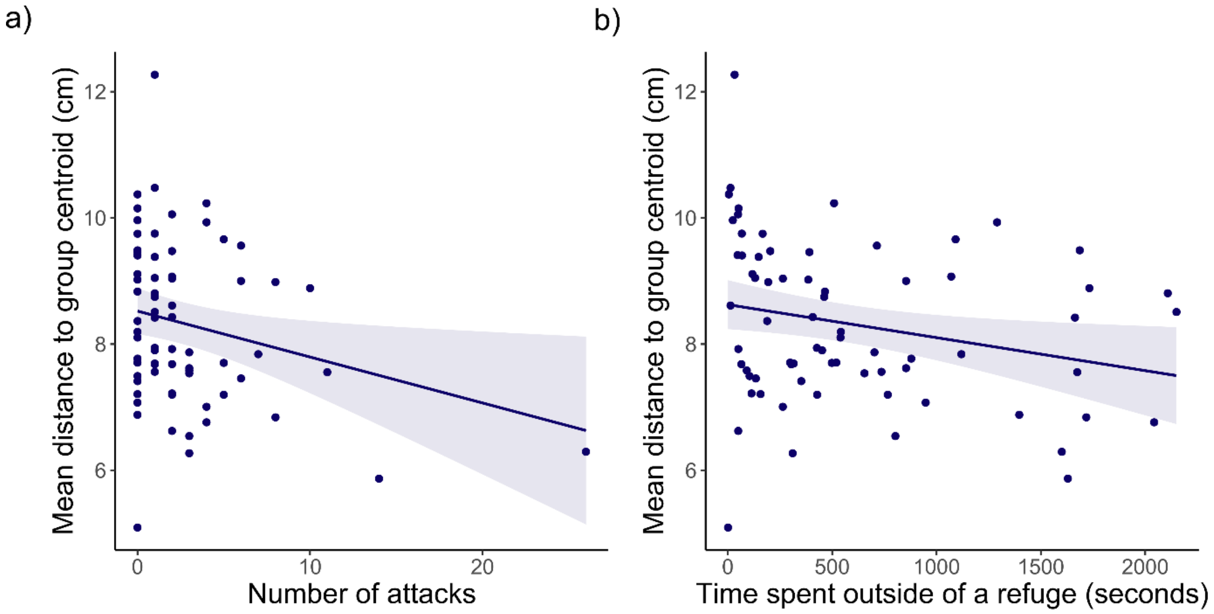
Figure 4.6: Influence of predator emergence on the mean distance of the prey group centroid from the deep end of the tank. The dashed horizontal line shows the mid-way point between the deep and shallow ends of the tank. The relationship is shown for both morning and afternoon predator-prey trials.

Table 4.5: Results from LMMs explaining variance in the mean distance moved by the prey group centroid every 10 seconds (a) and the mean distance of the prey group centroid from the deep end of the tank (b) over the course of a trial.

	Common model structure	**Additional predator behaviour explanatory variable**	**df**	**AICc**	**ΔAICc**
a)	Mean distance moved by group centroid every 10 seconds ~ Repeat + Predator-prey trial x Trial order + SBL	Predator emergence (binary variable)	10	456.2	0.00
		None (baseline model)	9	457.5	1.33
		Predator emergence (binary variable) x Predator-prey trial	11	458.4	2.24
		Boldness (in trials without prey)	10	459.7	3.49
		Boldness (in trials without prey) x Predator-prey trial	11	462.0	5.83
b)	Mean distance of group centroid from the deep end of tank ~ Repeat + Predator-prey trial x Trial order + SBL	Predator emergence (binary variable) x Predator-prey trial	11	709.1	0.00
		Predator emergence (binary variable)	10	710.9	1.88
		None (baseline model)	9	714.9	5.93
		Boldness (in trials without prey)	10	717.2	8.23
		Boldness (in trials without prey) x Predator-prey trial	11	719.3	10.38

4.4.6 Relationships between predator and prey behaviour: trials including prey in which pike cichlids emerged from the refuge

During predator-prey trials in which the predator left the refuge at least once, the mean distance of prey to the group centroid was negatively correlated with both the time spent outside of a refuge by the predator and the number of times the predator attacked prey in the same trial (**Fig. 4.7a-b**). Models including either the time spent outside of a refuge or the number of attacks as an explanatory variable received more support from the data than a baseline model without a predator behaviour explanatory variable, but there was no evidence for an effect of the proportion of time the predator spent near the prey or the mean boldness levels of individual pike cichlids in trials without prey (**Table 4.6a**). Conversely, model comparisons indicated that there were no statistically important relationships between the mean nearest neighbour distance of prey and the behaviour of pike cichlids (**Table 4.6b**). All models featuring the time spent by predators outside of a refuge, the number of attacks made or the proportion of time spent near prey received less support than the baseline model which included only repeat, the standard body length of the predator, predator-prey trial, trial order and the predator-prey trial x trial order interaction (**Table 4.6b**). Similarly, there was no evidence for any relationships between predator behaviour and the mean length-width ratio of the minimal bounding box encompassing the prey group (**Table 4.6c**).



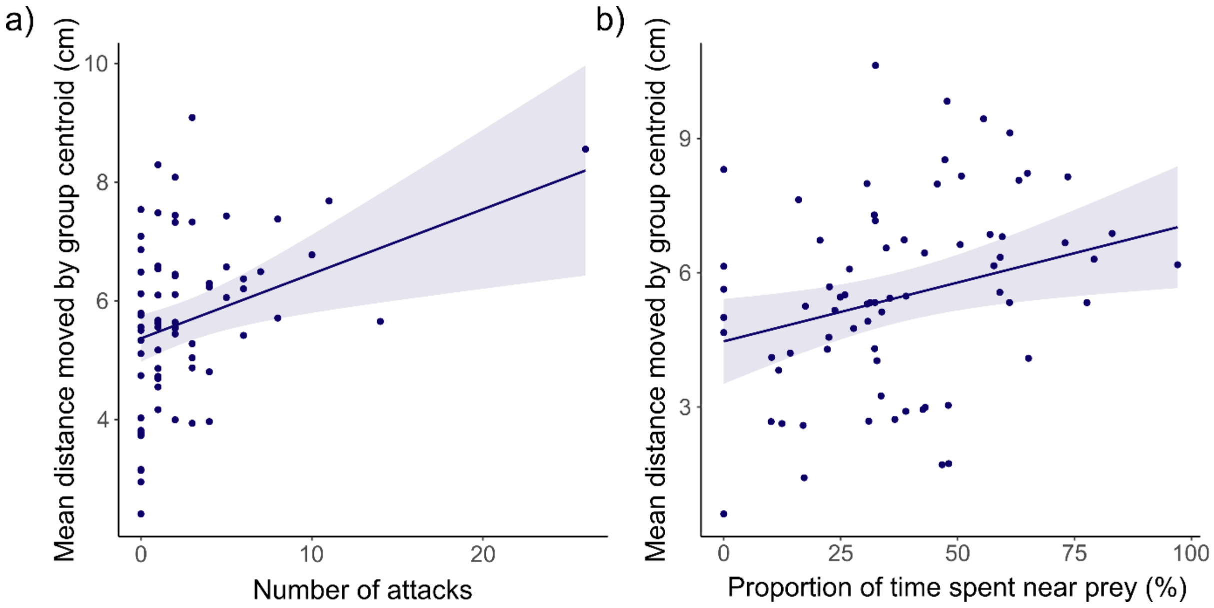
<u>**Figure 4.7:**</u> Relationship between the number of attacks on prey (a) and the time spent outside of a refuge by the predator (b) on the mean distance of individual prey to the prey group centroid. Plots show predicted values from models including non-interacting main effects for the number of attacks (a) and the time spent outside of a refuge (b), which were obtained by using mean values for all other explanatory variables in the model (**Table 4.6**). The shaded area represents 95% confidence intervals surrounding model predictions.

Table 4.6: Results from LMMs used to explain variance in the mean distance to the prey group centroid (a) and the mean nearest neighbour distance (b) over the course of a trial.

	Common model structure	**Additional predator behaviour explanatory variable**	**df**	**AICc**	**ΔAICc**
a)	Mean distance to the group centroid ~ Repeat + Predator-prey trial x Trial order + SBL	No. of attacks	10	231.7	0.00
		No. of attacks x Predator-prey trial	11	231.8	0.08
		Time spent outside of a refuge	10	232.2	0.47
		Time spent outside of a refuge x Predator-prey trial	11	233.9	2.24
		Boldness (in trials without prey)	10	233.9	2.25
		None (baseline model)	9	234.1	3.73
		Proportion of time spent near prey	10	235.8	4.17
		Boldness (in trials without prey) x Predator-prey trial	11	236.4	4.72
		Proportion of time spent near prey x Predator-prey trial	10	236.5	4.80
b)	Mean nearest neighbour distance ~ Repeat + Predator-prey trial x Trial order + SBL	None (baseline model)	9	152.3	0.00
		Time spent outside of a refuge	10	158.1	5.79
		Boldness (in trials without prey)	10	158.3	5.97
		Proportion of time spent near prey	10	158.4	6.12
		No. of attacks	10	159.6	7.31
		Boldness (in trials without prey) x Predator-prey trial	11	162.4	10.05
		Time spent outside of a refuge x Predator-prey trial	11	162.8	10.50
		Proportion of time spent near prey x Predator-prey trial	11	163.1	10.75
		No. of attacks x Predator-prey trial	11	166.1	13.74
c)		None (baseline model)	9	115.8	0.00

	Mean length-width ratio of minimal bounding box encompassing prey group ~ Repeat + Predator-prey trial x Trial order + SBL	Time spent outside of a refuge	10	116.1	0.33
		Proportion of time spent near prey	10	117.1	1.30
		Proportion of time spent near prey x Predator-prey trial	11	117.1	1.31
		Boldness (in trials without prey)	10	117.3	1.53
		No. of attacks	10	117.6	1.66
		Time spent outside of a refuge x Predator-prey trial	11	117.9	2.13
		Boldness (in trials without prey)	11	118.2	2.38
		No. of attacks x Predator-prey trial	11	119.4	3.56

There was a positive relationship between the mean distance moved by the prey group centroid every 10 seconds and both the number of attacks made by the predator (**Fig. 4.8a**) and the proportion of time spent near prey (**Fig. 4.8b**), but there was no effect of the time spent outside of a refuge during trials with prey or boldness in trials without prey (**Table 4.7a**). Models including the number of attacks and the proportion of time spent near prey received substantially more support from the data than the baseline model, and performed better than more complex versions of the same models including an interaction between the relevant predator behaviour variable and predator-prey trial (**Table 4.7a**). For the mean distance of the prey group centroid from the deep end of the tank, all models including explanatory variables for predator behaviour during trials with prey or predator boldness in trials without prey received less support from the data than the baseline model (**Table 4.7b**).



<u>Figure 4.8:</u> Relationship between the number of attacks on prey (a) and the proportion of time the predator spent near prey (b) on the mean distance of moved by the prey group centroid every 10 seconds. Plots show predicted values from the two models receiving most support from the data (**Table 4.7a**), which were obtained by using mean values for all other explanatory variables in the model. The shaded area represents 95% confidence intervals surrounding model predictions.

Table 4.7: Results from LMMs explaining variance in the mean distance moved by the prey group centroid every 10 seconds (a) and the mean distance between the prey group centroid and the deep end of the tank (b) over the course of a trial.

	Common model structure	**Additional predator behaviour explanatory variable**	**df**	**AICc**	**ΔAICc**
a)	Mean distance moved by group centroid every 10 seconds ~ Repeat + Predator-prey trial x Trial order + SBL	No. of attacks	10	254.5	0.00
		Proportion of time spent near prey	10	256.1	1.67
		No. of attacks x Predator-prey trial	11	256.6	2.17
		Proportion of time spent near prey x Predator-prey trial	11	258.7	4.20
		None (baseline model)	9	259.4	4.95
		Boldness (in trials without prey)	10	262.1	7.60
		Time spent outside of a refuge	10	262.1	7.66
		Time spent outside of a refuge x Predator-prey trial	11	264.5	10.07
		Boldness (in trials without prey) x Predator-prey trial	11	264.5	10.07
b)	Mean distance between group centroid and deep end of tank ~ Repeat + Predator-prey trial x Trial order + SBL	None (baseline model)	9	375.8	0.00
		Time spent outside of a refuge	10	376.9	1.07
		Time spent outside of a refuge x Predator-prey trial	11	377.4	1.53
		Boldness (in trials without prey)	10	378.3	2.41
		Proportion of time spent near prey	10	378.6	2.76
		Boldness (in trials without prey)	11	379.6	3.73
		Proportion of time spent near prey x Predator-prey trial	11	380.0	4.18
		No. of attacks x Predator-prey trial	10	381.3	5.51
		No. of attacks x Predator-prey trial	11	384.7	8.84

4.5 Discussion

By investigating how shoals of guppies adjust their behaviour following exposure to their main predator, the pike cichlid, the results of this study highlight how the intensity of prey anti-predator responses covaries with predator behaviour. Repeated observations of the pike cichlids in experimental pools without prey confirmed that individual predators differed consistently in the time taken to leave the refuge, indicating that individual predators varied in their risk-taking tendencies or boldness (Ioannou, Payne and Krause, 2008; Wilson *et al*., 2011; Balaban-Feld *et al*., 2019a). However, during trials with prey, only the proportion of time pike cichlids spent near prey differed consistently between individuals when trials from within the same day were analysed separately. Over the course of a trial, the mean intensity of the prey anti-predator response was also correlated with the behaviour of the predator within the same trial, but not with the boldness levels of individual predators as assessed during trials without prey. Mean shoal activity (the distance moved by the prey group centroid) was higher during trials in which pike cichlids spent a greater proportion of their time near prey, indicating that prey were responsive to an aspect of predator behaviour which differed consistently between individual predators. Additionally, when predators left the refuge during morning trials, which were conducted following a brief period of visual contact between the predator and the prey, guppies formed more cohesive and less elongated shoals compared to morning trials in which the predator never emerged. During afternoon trials, which commenced after pike cichlids and guppies had been in visual contact for 4-7 hours, these relationships were absent, suggesting that prey acclimatised to the presence of the predator after an extended period of exposure. By contrast, prey adjusted their shoaling response to behavioural variation within the subset of predators which did leave the refuge, irrespective of the period of time predators and prey were exposed to one another: in both morning and afternoon trials, greater shoal cohesion was associated with reduced refuge use and more frequent attacks by the predator. These results suggest that the intensity of prey anti-predator responses was more strongly predicted by the current behaviour of pike cichlid predators during a given trial with prey, rather than by the boldness levels of individual predators, as determined in a separate trial without prey. These findings therefore contrast with expectations based on the previously reported link between variation in the boldness and activity of individual predators and the risk they pose to prey (Ioannou, Payne and Krause, 2008; Toscano and Griffen, 2014).

During trials when prey were present, the individual-level repeatability of predator behaviour was estimated both by analysing all trials together (including trials from within the same day) and by splitting the analysis between morning and afternoon trials. By maintaining a longer inter-trial interval, the split analysis adheres more closely to the definition of animal personality variation which states that inter-individual differences in behaviour must remain repeatable over time (Réale *et al.*, 2007). Of all the predator behaviour variables which were found to influence the prey's anti-predator response, the proportion of time spent near prey was the only trait which also differed repeatably between individual pike cichlids in the both the combined and split analyses (the proportion of time spent near prey was moderately repeatable between individuals in afternoon trials but not morning trials). Given the low sample sizes in the split analysis, this represents relatively strong evidence that individual predators differed consistently in this trait across multiple days. Significant repeatability in the proportion of time individual pike cichlids spent near prey suggests that individual predators differed consistently in their propensity to actively approach within close range of the prey shoal, independently of their refuge use. The relationship between inter-individual variation the proportion of time predators spent near prey and the time taken to leave the refuge in trials without prey was also highly uncertain, making it difficult to be conclusive about the relationship between inter-individual variation in the response to prey and boldness.

In contrast to the proportion of time spent near prey, there was relatively weak evidence to suggest that pike cichlids differed consistently in other aspects of their behaviour during trials with prey. There were significant repeatable differences between individual pike cichlids in whether or not predators left the refuge and in the time spent outside of a refuge when morning and afternoon trials were analysed jointly, but not when trials from within the same day were considered separately. While it is difficult to exclude the possibility that the lack of statistically significant repeatability in the split analysis was the result of a reduced sample size, a lack of consistency across multiple days may also imply that the refuge use tendencies of individual predators are only predictable over relatively short time-scales. Although decisions to leave a refuge typically reflect the relative costs and benefits of continued safety versus potentially risky foraging, they can be influenced by an animal's current energetic or nutritional state (Clark, 1994; Balaban-Feld *et al.*, 2019b). Inconsistency might therefore have arisen due to fluctuating levels of motivation, which might be more variable over a time-scale of days. In addition to measures of refuge use, there was no evidence for consistent inter-individual differences in the number of attacks on prey or the rate of attack in either the combined or split analyses. Compared with other aspects of predator behaviour, such as the choice of which prey to target within a group, the timing of attacks by predators on prey is often highly variable (Penry-Williams, Ioannou and Taylor, 2018). While previous studies have suggested that individual predators differ consistently in the time taken to attack prey (McGhee, Pintor and Bell, 2013), in this study, any stable inter-individual variation in the total number and rate of attacks could have been overwhelmed by other complicating factors. For example, if predators base their attack decisions on fine-scale aspects of prey behaviour, but also induce behavioural changes in prey, subtle differences in how predator and prey responded to one another as a trial progressed could have contributed to the lack of consistency in individual attack rates.

The presence of predation cues typically elicits greater cohesion in prey groups, reducing the level of repulsion which occurs between individual prey over short distances and increasing attractive forces between prey which are far apart (Schaerf, Dillingham and Ward, 2017). The intensity of predation pressure is also associated with pronounced differences in shoal cohesion between distinct guppy populations (Botham *et al.*, 2008; Herbert-Read *et al.*, 2017a; Ioannou, Ramnarine and Torney, 2017), implying that predation by pike cichlids and other predators is likely to select for tighter shoaling behaviour in this species (Magurran *et al.*, 1992). Behavioural feedback between the predator and the prey is likely to have occurred in this study, making it difficult to disentangle the influence of predator behaviour on prey from the reverse effect of prey on predators. However, the reduction in the mean distance of prey to the group centroid, which was observed in morning trials in which pike cichlids emerged from the refuge, is consistent with a differential prey response to the perceived threat posed by the predator. Furthermore, both the total time spent outside of the refuge and the number of attacks made by the predator were negatively correlated with the mean distance of prey to the shoal centroid. This indicated that prey were sensitive to behavioural variation within the subset of predators that emerged from the refuge and were thus visible to prey. By contrast, the mean nearest neighbour distance of guppies within the prey group was unrelated to the behaviour of pike cichlids. These results suggest that the effect of predator refuge use or attack frequency on group cohesion is likely to have been on the overall shape or configuration of the shoal, rather than on inter-individual distances within the prey group. The negative association observed between whether or not pike cichlids emerged from the refuge and the mean length-width ratio of the prey group (during morning trials) supports this conclusion, as it indicates that prey formed less elongated shoals in the presence of a predator. When viewed together, these findings are reminiscent of previous work which demonstrates that prey shoals adopt a more compact shape when predators are present in the immediate vicinity (Magurran and Pitcher, 1987; Romenskyy *et al.*, 2019).

The impact of predator behaviour on prey anti-predator responses was not limited to the cohesion and shape of the prey shoal. The mean distance moved by the prey group was higher when prey were exposed to pike cichlids which spent a greater proportion of their time within close proximity. Although prey often show reduced levels of activity when exposed to non-directional cues indicating increased risk (e.g. conspecific alarm cues, Schaerf, Dillingham and Ward, 2017), this result resembles the increases in speed which typically occur in shoaling fish when prey are confronted with an actively stalking or striking predator, and move away from the direction of the immediate threat (Magurran and Pitcher, 1987; Kent *et al*., 2019). The mean position of the prey shoal also shifted towards the shallower end of the water depth gradient during trials in which pike cichlids emerged from the refuge, which is consistent with evidence suggesting that shallower areas of water represent less risky habitats in the guppies' natural environment (Croft *et al*., 2006). Though the shift to shallower water was not particularly strong, and was more substantial in afternoon trials, any effect of perceived risk on the average value of this variable in a trial may have been complicated by anti-predator responses which occur rapidly over a short time-scale, including evasive movements away from the approaching predator or freezing in the aftermath of an attack (Magurran and Seghers, 1990; Brown *et al*., 2009). As well as the prey anti-predator behaviours quantified in this study, guppies are also known to respond to pike cichlids by spending more time at water's surface (Botham *et al*., 2008). Although accurately quantifying the proportion of time guppies spent near the surface was not possible in this study, it would have been interesting to test whether prey also responded to variation in predator behaviour by adjusting their position in the water column. Despite this, it was still notable that there were no relationships between the boldness levels of individual predators and the strength of any of the measured prey anti-predator responses. This suggests that variation in the risk-taking tendencies of individual pike cichlids, as measured in trials without prey, was not relevant to prey's perception of risk.

Differences in the relationship between predator and prey behaviour between morning and afternoon trials suggested that guppies acclimatise to the presence of a pike cichlid relatively quickly when they are inaccessible to the predator, as is often the case in shallower areas of river pools within their natural environment (Mattingly and Butler, 1994; Croft *et al*., 2006). Although the time of day when trials were conducted was correlated with the effect of increasing exposure, a predator-prey trial (i.e. morning or afternoon) x trial order (i.e. the first, second or third recording time within a day) interaction was included in models. By allowing the effect of trial order to vary between the morning and the afternoon, this interaction term was designed to capture a potentially cyclical effect of the time of day on predator and prey behaviour, in which the predatory activity of pike cichlids is expected to peak at approximately midday (Endler, 1987). Whereas in the morning trials the emergence of pike cichlids from the refuge was associated with greater shoal cohesion, the degree of group cohesion observed during afternoon trials remained the same regardless of whether or not the predator left the refuge, and matched the levels recorded in morning trials during which the predator was not visible to prey. Within the subset of predators that did emerge from the refuge, there was no overall change in the amount of time spent outside of a refuge between the morning and the afternoon trials. The reduced responsiveness of prey during afternoon trials was therefore unlikely to have been driven by a change in the total amount of time predators spent outside of the refuge. Conversely, there was no difference between morning and afternoon trials in the strength of the negative relationship between the number of attacks made by the predator or the time spent by the predator outside of a refuge and the mean distance to the group centroid. These contrasting results suggest that prey become less responsive to the sight of a predator outside of the refuge over time, but remain sensitive to the behaviour of predators which do emerge, which should more accurately reflect immediate levels of danger. While the reduced responsiveness of prey to the emergence of a pike cichlid from the refuge following sustained exposure is reminiscent of habituation to a non-threatening stimulus, this result could also be explained by optimal risk allocation theory, which predicts that strength of prey anti-predator behaviour should decline as the duration of exposure to risk increases (Lima and Bednekoff, 1999; Ferrari, Sih and Chivers, 2009). Regardless of the mechanism, a decline in responsiveness to low-risk predator cues over time could benefit prey by reducing the opportunity costs associated with a heightened anti-predator response (Rodríguez-Prieto, Martín and Fernández-Juricic, 2010).

An important limitation of the artificial pools used in this experiment is that the ability of prey to avoid the predator entirely is restricted. Within the guppies’ natural environment there are typically shallow zones on the margins of river pools, which represent relatively safe habitats, since predators tend to be found within areas of deeper water and the risk of capture by aquatic predators is reduced with decreasing water depth (Mattingly and Butler, 1994; Botham *et al*., 2005; Croft *et al*., 2006). By including a water depth gradient within the central tank enclosing the prey shoal, the artificial pools used here replicate these environmental features to a limited extent. One likely difference between the experimental pools and the situation in the wild is that retreating to a large shallow area within a natural river pool may allow guppies to avoid close contact with predators altogether, enabling them to relax their anti-predator response. These considerations help to emphasise the wider point that although the fitness costs to prey of sustaining an elevated anti-predator response can be substantial over a prolonged period, in natural systems, prey are often able to avoid or compensate for these negative effects by modifying multiple other aspects of their behaviour (Lima, 1998; Lind and Cresswell, 2005). Whether or not heightened anti-predator responses ultimately translate into fitness costs (i.e. non-lethal or non-consumptive effects) is highly context-dependent, and is influenced by a range of factors, including the costs and benefits of the alternative behavioural options available to prey as well as the environmental context (Weissburg, Smee and Ferner, 2014; Sheriff *et al*., 2020). For example, the abundance and profitability of resources within safe habitats can have an important effect on whether it is costly for prey to avoid predators by altering their habitat use (Donelan, Grabowski and Trussell, 2017). Moreover, the strength of any potential non-lethal effects in aquatic environments is likely to be determined by properties of the habitat which influence the reliability of information gained from visual predator cues, such as the structural complexity of vegetation, the level of turbidity or the presence of visual noise generated by dynamic lighting (Miner and Stein 1996; Matchette, Cuthill and Scott-Samuel, 2018; Chamberlain and Ioannou, 2019). To quantify the impact of predator personality on the strength of non-lethal effects, future studies should aim to expose prey to predators over a much longer period, and conduct experiments in settings which accurately reproduce other key attributes of the predator and prey's shared environment.

Chapter 5:

Using robotic prey to test the effect of prey unpredictability on predator behaviour

Blue acara cichlid (*Aequidens pulcher*),
the species of predatory fish studied in this chapter.
Photograph: A. W. Szopa-Comley.

5.1 Abstract

Capturing evasive prey can be challenging, but with repeated experience predators can potentially become more successful by learning to refine their attack and pursuit behaviour. The disruptive effect of unpredictable prey escape behaviour on learning by predators has been proposed as a possible functional explanation for variability in the angle of escape by prey. To test whether predictability in prey escape responses can influence predator learning, I developed a novel experimental system in which artificial robot-controlled prey items were programmed to flee in response to an attack from individual blue acara cichlids (*Aequidens pulcher*). Using this approach, it was possible to experimentally manipulate the prey's initial escape direction relative to the approach direction of the predator, and repeatedly present individual predators with prey that escaped in either predictable or unpredictable directions from one experimental trial to the next. Over twenty successive trials, there was no direct evidence to suggest that the change in predator behaviour with increasing experience was influenced by the predictability of the prey's escape angle. However, in the predictable treatment, there was a positive relationship between the prey's escape angle and the maximum speed of the approaching predator: predators approached prey programmed to escape directly away from them at higher speeds than prey programmed to escape at an acute angle, of ninety degrees or less. This relationship was absent in trials with unpredictable prey, suggesting that predators modified their approach speed when relatively certain about the direction prey would escape in. Predators approaching at high speeds also captured the prey more quickly regardless of treatment and escape angle, but when pursuing prey which escaped at an acute angle, there was no clear cost to a rapid approach. While aspects of these results are consistent with an effect of prey predictability on predator behaviour, more empirical studies are needed to clarify the specific impact of unpredictable prey escape trajectories on learning by predators.

5.2 Introduction

Learning, defined functionally as changes in individual behaviour based on experience (Shettleworth, 2010), enables organisms to flexibly adjust their behaviour in response to novel challenges (Brown and Chivers, 2005; Kelley and Magurran, 2011; Morand-Ferron, 2017). The lethal impact of predation generates strong selective pressure for prey to modify their behaviour following exposure to cues which reliably indicate increased risk (Lima and Dill, 1990; Bouskila and Blumstein, 1992), but since many attacks by predators ultimately end with the prey evading capture (Vermeij, 1982), predators should also be under selection to dynamically respond to prey and to learn from recent hunting experience (Abrams, 1986; Lima, 2002; Sih, 2005). While there is evidence that prey can learn to recognise novel predators (Chivers and Smith, 1994; Griffin, Evans and Blumstein, 2001) or adjust their anti-predator behaviour to match predictable changes in risk (Ferrari and Chivers, 2009), there have been far fewer experimental studies investigating the importance of learning in shaping predator behaviour (Kelley and Magurran, 2011). In particular, there has been little research on the role of learning in modulating predator attack or pursuit strategies. As understanding the evolution of prey defences often depends on an accurate picture of the cognitive processes influencing predator decision-making, readdressing this imbalance can potentially shed light on the adaptive significance of prey escape strategies.

The learning abilities of predators are relevant to the evolution of a wide range of anti-predator adaptations in prey, but have been studied most extensively in relation to prey colour patterns. For visual predators searching for camouflaged prey, experience with specific prey types can facilitate the formation of search images, enabling locally abundant prey types to be detected more rapidly (Pietrewicz and Kamil, 1979). By focusing predators' attention on the features found in locally abundant prey types, search image formation can reduce predation on rare phenotypes, and help explain patterns of frequency-dependent switching between alternative prey types, as well as the evolution of polymorphism within prey populations (Bond and Kamil, 2002). Knowledge of predator cognition, including learning, is also crucial when attempting to understand the selection pressures generating diversity in warning signals, which function in part to accelerate the formation of learned avoidance of unpalatable prey (Ruxton, Sherratt and Speed, 2004). Although associations between prey colour patterns and noxious chemical defences are formed more strongly for prey phenotypes which predators encounter more frequently, which is thought to result in positive frequency-dependent selection favouring convergence on a single aposematic morph (Lindström *et al*., 2001; Chouteau, Arias and Joron, 2016), there is nevertheless evidence for considerable diversity in warning colours and patterns (Briolat *et al*., 2018). Inter- or intra-specific variation in learning by predators has been suggested as one of the many possible causes for this apparent discrepancy between theory and evidence (Rowland, Fulford and Ruxton, 2017), in addition to the possibility that predators might also learn about prey in more sophisticated ways than is typically considered by the mathematical models which predict monomorphic prey populations (Skelhorn, Halpin and Rowe, 2016). Correspondingly, models which assume more complex predator cognition incorporating the need for predators to gather information about unfamiliar prey types predict a broader range of evolutionary outcomes (Aubier and Sherratt, 2015). Much less is known about the possible impact of predator learning on prey behavioural traits, but there is evidence that predators can progressively improve their attack and prey handling efficiency throughout their development (Chen *et al*., 1996) and following exposure to specific prey types (Croy and Hughes, 1991). Predators with prior experience are also more successful in capturing evasive prey compared to those lacking any exposure to live prey (Reid, Seebacher and Ward, 2010), raising the possibility that predators can refine aspects of their approach and pursuit behaviour over multiple repeated encounters.

As learning relies on frequent exposure to predictable cues, prey can potentially counteract predator learning by behaving unpredictably (Mitchell, 2009; Herbert-Read *et al*., 2017b; Moore *et al*., 2017). When faced with an imminent threat from an approaching predator, prey have few options but to attempt to escape by performing a rapid burst of acceleration. In the initial moments of an escape manoeuvre, theoretical models predict that prey should select a single optimal trajectory which maximises the distance from an approaching predator (Weihs and Webb, 1984, Domenici, 2002), but in empirical studies initial prey escape angles are often surprisingly variable (Walker *et al*., 2005; Domenici *et al*., 2008; Domenici, Blagburn and Bacon, 2011a; Hitchcock *et al*., 2015; Nair *et al*., 2017). Deviating from the optimal escape angle can have important consequences for prey survival (Walker *et al*., 2005; Corcoran and Conner, 2016), and it has been suggested that the existence of variability in initial escape angles can be explained by biomechanical or sensory constraints in prey (Domenici, Blagburn and Bacon, 2011b). However, variability within a limited angular range might also represent an anti-predator strategy aimed at generating unpredictability (Domenici, Blagburn and Bacon, 2011b). Whereas predators might be able to learn to anticipate the movements of prey which repeatedly escape at a fixed angle relative to their approach, initial escape responses which incorporate an element of unpredictability could prevent predators from learning to anticipate the directional heading of their target over the course of multiple attacks (Humphries and Driver, 1970; Edut and Eilam, 2004; Domenici, Blagburn and Bacon, 2011a). If unpredictability prevents learned improvements in the performance of the predator, this type of defence could maintain a high probability of escape and force predators to target alternative prey.

Further insight into the effect of predictability in escape direction can be found in controlled experiments in which human ‘predators’ target continuously moving virtual prey. In these studies, the survival of moving prey is enhanced by abrupt and unpredictable changes in direction (Jones, Jackson and Ruxton, 2011). Erratic changes in the prey’s direction can also act synergistically with prey density to intensify the confusion effect (Scott-Samuel *et al*., 2015). When prey movement rules incorporate both erratic turns and unpredictable changes in speed, increased path complexity also reduces the ability of human subjects to accurately target virtual prey (Richardson *et al*., 2018), but it is unknown whether the survival advantage conferred by unpredictable motion also applies broadly against non-human predators, or specifically to the escape responses of prey which are initially stationary rather than in continuous movement. This situation is widespread in nature, as many prey move little when foraging, before reacting quickly when a predator is detected.

Numerous cryptic prey taxa may also initially remain motionless to avoid detection by predators, eventually fleeing only once a predator is in the immediate vicinity (Cooper and Blumstein, 2015; Møller, Liang and Samia, 2019). Optimal prey escape behaviour in this context has also been explored extensively using mathematical models of flight initiation distance (Ydenberg and Dill, 1986; Broom and Ruxton, 2005; Cooper and Frederick, 2007). Although a wide variety of prey appear to employ this escape strategy, no studies have yet examined the impact of unpredictability in initial prey escape angles on learning over repeated interactions with predators.

Many predator-prey interactions are typified by dynamic behavioural feedback between the attacker and the target (McGhee, Pintor and Bell, 2013), making it difficult to disentangle the effects of prey defences on predators from the impact of predator behaviour on prey using a purely observational approach. Without experimentally manipulating prey behaviour, it can be challenging to isolate the effect of prey anti-predator strategies from the impact of other phenotypic differences, including variation in traits such as body size or subtle differences in body posture, which can influence the decision-making of predators during an attack (Mattingly and Butler, 1994; Krause and Godin, 1996). The limitations of observational studies can be overcome by presenting real predators with standardised virtual prey stimuli, whose movements and behaviour can be precisely controlled and experimentally manipulated (Bond and Kamil, 2002; Ioannou, Guttal and Couzin, 2012; Duffield and Ioannou, 2017; Hogan, Cuthill and Scott-Samuel, 2017; Ioannou *et al.*, 2019). However, previous experiments using this approach have been based on unresponsive simulated prey which are unable to escape from or otherwise react to an approaching predator, making it difficult to study prey escape behaviour using these techniques.

In order to test the effect of unpredictability in prey escape angles on predator behaviour over multiple interactions, I therefore developed a novel experimental system in which artificial robot-controlled prey items were programmed to flee from blue acara cichlid (*Aequidens pulcher*) predators, once the predator had approached within a set distance. Blue acaras are opportunistic predators with a broad diet, but often actively pursue highly evasive prey such as Trinidadian guppies (Krause and Godin, 1996; Botham *et al*., 2006). After an initial period in which groups of blue acara cichlids were trained to attack the prey (*training phase*), individual predators were assigned to one of two experimental treatments and repeatedly presented with prey over twenty successive experimental trials (*test phase*). Prey in the two treatments differed in the consistency of their escape behaviour from trial-to-trial: in the predictable treatment, prey escaped in the same direction relative to the predator's approach from one trial to the next, whereas in the unpredictable treatment, prey were programmed to flee in random directions over successive trials (**Fig. 5.1**). To successfully capture prey, pursuit predators must respond to changes in prey direction which occur at the start of, or during a chase (Ghose *et al*., 2009; Kane, Fulton and Rosenthal, 2015; Clemente and Wilson, 2016). Across trials with predictable prey, predators had the opportunity to gain reliable information about the prey's likely escape direction, but in the unpredictable treatment, the escape angle of the prey in previous trials was not a reliable indicator of its escape direction in future encounters. In both treatments, the prey remained motionless until the attacking predator had approached within a pre-specified distance, and escaped in straight line following the initial attack. If unpredictability in the initial escape angle of prey impedes learning by predators, I predicted that the blue acara cichlids would show limited improvement in their performance over successive trials in the unpredictable treatment. By contrast, in the predictable treatment, predators would be expected to show more pronounced adjustments in their approach and pursuit behaviour with increasing experience. Consequently, if unpredictability is an effective prey defence at this stage of the predator-prey interaction, predator behaviour should be influenced by an interaction between treatment (prey predictability) and trial number.

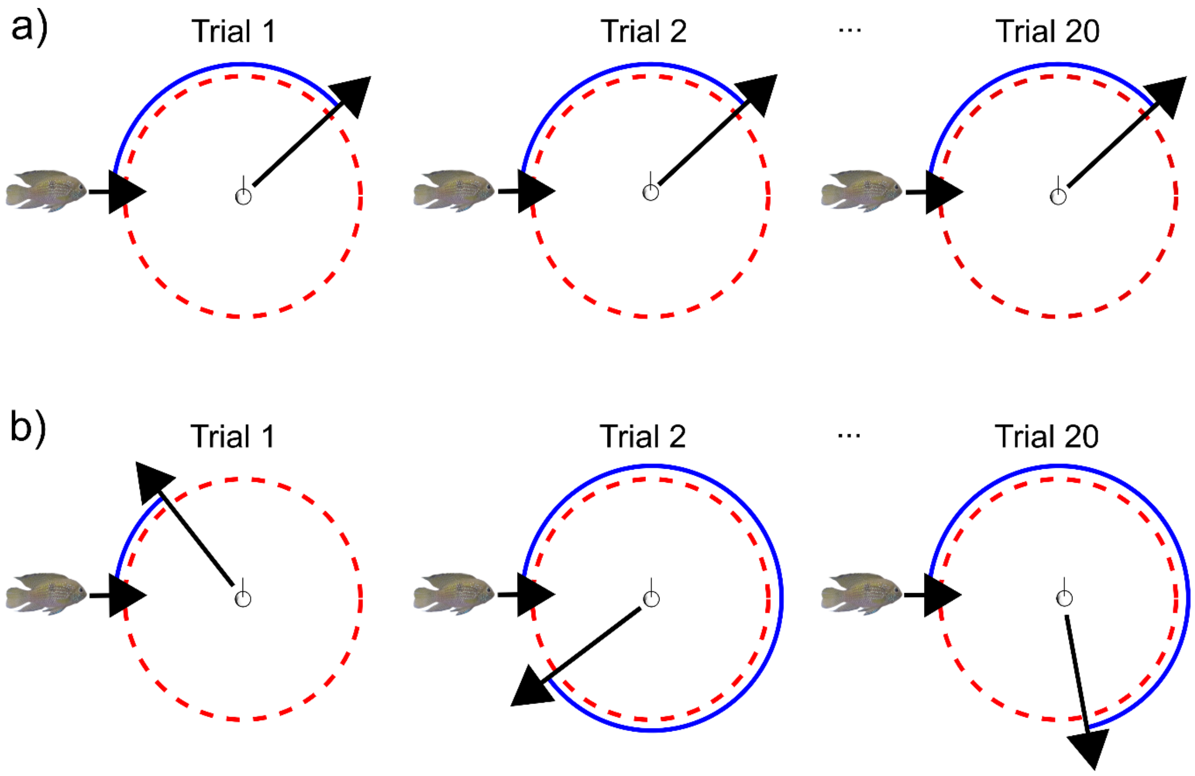


Figure 5.1: Use of robot-controlled prey to manipulate the predictability of prey escape angles from trial to trial. In the predictable treatment (a), prey escape angles (relative to the approaching predator, indicated by the blue arcs) were kept constant for individual predators from trials one to twenty, but varied between individuals. For predators allocated to the unpredictable treatment (b), the prey escape angle varied randomly from trial to trial.

5.3 Methods

5.3.1 Experimental subjects and housing

A total of twenty-eight blue acara cichlids (*Aequidens pulcher*) were tested in the experiment (median standard body length: 6.2 cm, inter-quartile range: 1.95 cm). As a maximum of 16 fish could be tested simultaneously, the experiment was first conducted with 16 fish in November and December 2018 and then repeated with an additional 12 fish in February and March 2019. Outside of the experimental period, fish were kept in glass tanks (width = 40 cm, length = 70.5 cm, height =

35.5 cm), with a daily 12h:12h dark:light cycle. The water temperature inside the tanks was kept at 26-27°C (+/- 0.5°C). Throughout the training and test phases of the experiment, groups of four fish were kept in a holding zone located at one end of the experimental arena. Groups comprised individual fish of different sizes, enabling individuals to be identified. Throughout the experiment, fish were fed *ad libitum* on aquarium fish pellets (ZM Systems, Large Premium Granular) at the end of each day of training or testing.

5.3.2 Experimental set-up and robotic prey system

The robotic prey system used in the experiment had five key components: a large rectangular experimental tank divided into a testing arena and a holding zone, a Bluetooth-controlled robot resting on a wooden platform suspended below the experimental tank, an artificial prey item located within the experimental tank itself, a webcam positioned above the tank and a Bluetooth-enabled laptop connected to the webcam via a USB cable. The testing arena and fish holding zone were situated within a large experimental tank made from aluminium (width = 127 cm, height = 36 cm, length = 238 cm). Within this external structure, an inner tank was constructed from white PVC walls (height = 35 cm, thickness = 0.8 cm) sealed to a white base made of compressed white foamed PVC (thickness = 0.2 cm) using aquarium sealant. This created a background with a high contrast enabling the movement of the predator to be detected using custom-built software. The smooth surface of the inner tank also allowed the robot-controlled artificial prey to move evenly across the arena, and avoided contact between water used to fill the arena and the outer aluminium tank. The inner tank was divided into a large rectangular experimental arena (width = 120.5 cm, length = 183 cm; **Fig. 5.2**), separated from a smaller holding zone by a white plastic divider, positioned at one end of the tank.

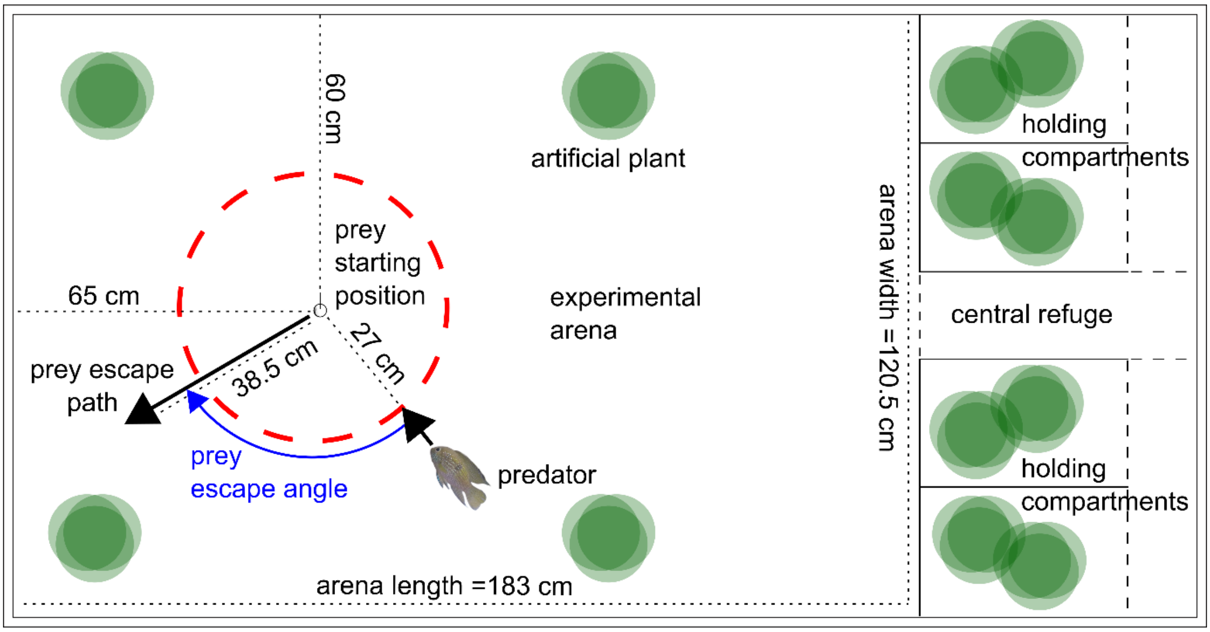
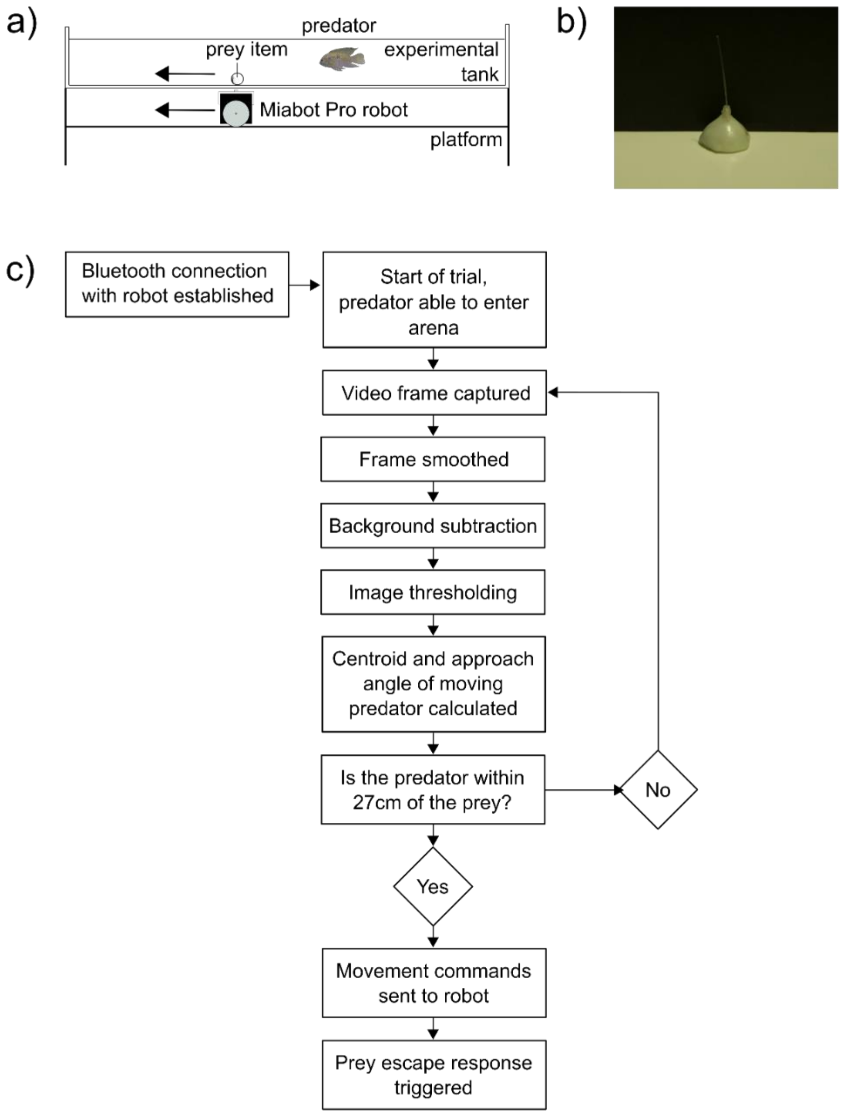


Figure 5.2: Scale diagram of the experimental arena, viewed from above. The red dashed line indicates the predator-prey distance (27 cm) at which the initially stationary prey item was programmed to escape from an approaching predator. Black arrows indicate the heading of the approaching predator and the escaping prey. Dashed lines indicate retractable doors, and dotted lines are used to indicate the dimensions of the arena. The prey escape angle (relative to the approaching predator) is shown in blue.

Throughout the duration of the experiment, including both the training and test phases (see below), fish were kept in the holding zone in groups of four individuals. The holding zone was sub-divided into four compartments (width = 25.75 cm, length = 41.5 cm each), with two compartments positioned either side of a central refuge (width = 16 cm, length = 55.5 cm, **Fig. 5.2**). Each compartment contained a cylindrical tube and two artificial plants to provide cover for the fish. Small pebbles (< 0.5mm diameter) were also scattered across the floor of each compartment and the central refuge to habituate the fish. Holding compartments were linked to the central refuge via a connecting corridor (width = 14 cm, length = 51.5cm), which bordered the external wall of the inner tank. The connecting corridor was separated from adjacent compartments and the central refuge by retractable doors, enabling fish to be transferred from their holding compartments to the central refuge without being caught in nets, thus minimising handling stress. The central refuge was covered by rigid black plastic mesh, and was also separated from the experimental arena by a retractable door.

The experimental arena contained a water heater attached to the wall furthest from the holding zone, and four artificial plants positioned near the edges. Trials were filmed using a camcorder (Panasonic SD 800, resolution: 1920 x 1080 pixels, frame rate: 25 frames per second) suspended approximately 225 cm above the experimental tank. A webcam (Logitech C920 USB Pro) was also secured 175 cm above the tank to monitor the movements of the predator during experimental trials. Throughout the experiment, the water depth in the experimental tank was kept at 15 cm, temperature was held constant at 27°C (+/- 0.5°C) and a 12h:12h light:dark cycle was maintained. Water was continually filtered and circulated throughout the entire tank using two Eheim Classic 600 external canister filters, which took in water via inflow pipes positioned in the corners of the arena closest to the heater and discharged water back into the holding zone.

A Bluetooth-controlled robot (MiaBot PRO BT v2, Merlin Systems Corp. Ltd.) located on a platform underneath the experimental arena was used to direct the movements of an artificial prey item situated within the arena itself (**Fig. 5.3a**). This type of wirelessly-controlled robot has previously been used to regulate the movements of a model predator in previous experiments with live fish (Swain, Couzin and Leonard, 2012), and comprised two wheels set within either side of a 7.5 cm cube containing the electronic circuitry, batteries and separate motors for each wheel. The artificial prey item itself consisted of a small amount of food (an approximately 5 mm x 8 mm piece of defrosted fish) attached to a length of transparent monofilament fibre (thickness = 1 mm, length = 4 cm) protruding from a cone-shaped white plastic base (diameter = 2.5 cm, cone height = 1.8 cm, **Fig. 5.3b**). Movement of the prey was controlled by the robot through a magnetic connection between neodymium magnets embedded in the base of the prey item, and another magnet embedded in a plastic hood secured to the top of the robot. In training or test phase trials in which the prey was programmed to respond to an approaching predator, the artificial prey item was placed in the same starting position within the experimental arena (60 cm from the horizontal sides of the experimental arena, 65 cm from the heater, and 118 cm from the entrance to the refuge; **Fig. 5.2**).



<u>Figure 5.3:</u> Overview of the robot prey experimental system. (a) Diagram (not to scale) showing a side-view of the experimental tank, with the Bluetooth-controlled robot situated on a platform underneath the tank. (b) Photo of the artificial prey item used in the experiment, shown against a dark background. (c) Schematic diagram showing steps involved in the program used to control how prey respond to an approaching predator.

To enable artificial prey to escape from an approaching predator, I created a custom-built program using the OpenCV library (version: 3.1.0) in python (version: 2.7.12), in order to integrate motion detection with control of the robot (**Fig. 5.3c**). Prior to an attack, the program continuously analyses video frames captured by the webcam positioned above the arena, monitoring any changes from one frame to the next which could indicate movement of the fish within the arena. As part of this process, each frame was first converted to grayscale and smoothed to filter out noise. Background subtraction was then used to calculate differences in pixel values between the current frame and a representation of the static background (i.e. the unchanging aspects of the experimental arena). The background was estimated using a running average, in which motion during more recent frames was weighted more heavily. Thresholding was then applied to the resulting image to isolate areas of the current frame which differed substantially from the background. Additional size filtering also ensured that any regions of movement below a pre-specified size threshold were disregarded, to make certain that noise was ignored and that the sole region of detected motion corresponded to the predator. The program then used this information to calculate the centroid of the predator in each frame, until the predator approached within a pre-specified radius of the prey's starting position (27 cm). Video frame processing was halted at this point, and movement commands were sent to the robot, based on the predator's angle of approach and the programmed prey escape angle. In both the training and the test phase, the escape response was triggered when a predator approached within 27 cm of the prey item; this distance was based on pilot trials conducted with different fish prior to the main experiment. In all escape responses, the robot was programmed to move a total of 38.5 cm in a straight line from its starting position towards the periphery of the tank. The initial prey escape angle, measured relative to the approaching predator, was the only aspect of the prey behaviour which varied between predictable and unpredictable treatments, in both the training and test phases.

Although the prey escape angle differed between trials, the program stored this angle as an input variable prior to the start of an experimental trial. Therefore, the only difference in the program between the predictable and unpredictable treatments did not have any bearing on the speed of the program during the trial itself. The turning time of the robot was also standardised across trials by including a 0.3 second time delay within the program, enforcing a consistent time lag in between the initial turn command being sent to the robot via Bluetooth, and the subsequent movement command which directed the robot to escape in a straight line. Data collected before the experiment with a high speed video camera (GoPro Hero 5, frame rate: 240 frames per second, resolution: 1280 x 720 pixels) indicated that the mean overall time delay between the predator moving within range and the robot moving was 0.7 seconds (n = 7, standard deviation: 0.08 seconds). This lag largely stemmed from a delay in the Bluetooth signal being acted upon by the robot, and not from video processing.

5.3.3 Boldness tests

Before being trained to attack artificial prey, the boldness of each individual fish was measured twice by recording the time taken to leave the refuge and enter the experimental arena (Ioannou, Payne and Krause, 2008; Bevan *et al*., 2018). The first and second boldness trial took place on two different days, separated by one day. Fish were transferred in groups of four to the holding compartments within the experimental tank on the afternoon before each testing day, and left overnight to habituate. Prior to the start of each trial, individual fish were moved to the central refuge and left to habituate for 5 minutes. After this point, the sliding door separating the refuge from the experimental arena was opened, allowing fish to exit the refuge and explore the experimental arena until the end of the trial. The trial was ended 15 minutes after the refuge door had been opened. Individual fish were tested in a randomised order. After the end of the first testing day, fish were transferred back to their home tanks, to ensure that the procedure for the second day was the same as that for the first. When the second round of boldness tests was completed, fish were returned to the holding zone of the experimental tank.

5.3.4 Training phase

After completing the two boldness tests, fish were progressively trained to approach and take food from the artificial prey item in a series of training trials, with three sequential training stages. As individuals in groups tend to behave more boldly than lone individuals (McDonald *et al*., 2016), training trials were conducted in the same groups that the fish were housed in, thereby increasing the speed of the training process. Groups progressed to the next training stage once a pre-specified criterion was reached (i.e. success was achieved in a set number of consecutive training trials), ensuring all groups were trained to a similar level. Before each training trial, groups of fish were transferred to the central refuge and left to habituate for 3 minutes. After 3 minutes, the sliding door separating the refuge from the experimental arena was opened, allowing fish to leave the refuge. Training trials lasted 10 minutes. At each stage of the training process, groups were subjected to three training trials per day.

In the first stage of the training phase, a static, baited prey item was positioned 25 cm from the entrance of the refuge, and surrounded by a small amount of food (12 cichlid pellets). Successful trials were those in which at least one fish from the group consumed at least one of the pellets surrounding the prey item. The criteria for progressing to the next stage was success in 6 consecutive training trials. Training trials in the second stage were identical to those in the first stage, but the prey item was placed at the centre of the experimental arena, in the same location as the test trials. In stage two (and stage three), successful trials were defined as those where at least one fish from the group consumed the food attached to the artificial prey item. Success in 10 consecutive trials was required to progress to the third and final stage of the training phase, which involved a responsive, baited prey item. In the third training stage, the robot-controlled prey item was programmed to initiate an escape response when a fish approached within the set distance (27 cm). The speed of the robot was programmed to escape at 7.9 cm s^{-1}, which is half the speed used in experimental trials. To ensure the training process did not bias the response of fish towards either of the two experimental treatments, groups experienced a mixture of training trials during the third stage. The training trials experienced by each group were split equally between prey which maintained the same escape angle in separate trials (predictable training trials), and prey which adopted random escape angles in each trial (unpredictable training trials). The order of predictable and unpredictable trials was pseudo-randomised, so that in the first and second training trials, groups of fish experienced one predictable and one unpredictable training trial, but the order of these two trials was randomised for each group. This way of determining trial order was repeated within each subsequent block of two consecutive training trials, until the fish had reached the criterion for progression to the test phase. To prevent prey moving directly back towards an attacking predator, in both treatments, escape angles were chosen from a uniform distribution from 45° to 315° (where 0° was defined as the approach angle of the predator).

5.3.5 Test phase

After completing the training phase, each fish was tested individually in twenty successive experimental trials against either predictable or unpredictable prey. At the start of each 10-minute long experimental trial, fish were transferred to the central refuge and left to habituate for 3 minutes. After 3 minutes, the sliding door separating the refuge from the experimental arena was opened, allowing fish to enter the experimental arena.

Experimental trials took place in three six-day blocks and one final two-day block, with a one-day gap occurring after the sixth, twelfth and eighteenth trial, i.e. after each block. Trials took place between 0900 and 1700, and the order individuals were tested in was also randomised on each day. Individual fish were allocated pseudo-randomly to either the predictable or the unpredictable treatment, subject to the added constraint that every group of four fish from the same holding compartment was split equally between the two treatments, with the largest two fish in each group being assigned to different treatments. In the unpredictable treatment, escape angles were generated randomly in each trial, and in the predictable treatment, trials with the same individual predator were conducted with a single randomly generated escape angle. As in the training phase, in both treatments, escape angles were chosen from a uniform distribution from 45° to 315° (where 0° was defined as the approach angle of the predator). Throughout all trials in the test phase, the escape response was initiated once the robot had approached within 27 cm of the prey, and the speed of the robot was set to an average speed along its escape trajectory of approximately 15.8 cm s^{-1}.

5.3.6 Video analysis

ToxTrac (version: 2.84) was used to extract the position of the predator in each video frame up to 30 seconds before and 30 seconds after the prey escape response was triggered (Rodriguez *et al.*, 2017). Video frames were 0.04 seconds apart. As there was minimal contrast between the artificial prey item and the experimental arena, the coordinates of the escaping prey were extracted manually from each frame using a custom-built program written in python (version: 3.6.9) using the OpenCV library (version: 4.1.1).

Multiple behavioural variables were also manually extracted from videos, including the time taken for the predator to leave the refuge, relative to the start of the trial. A measure of the predator's motivation to pursue prey within each trial was also obtained from videos by recording the time taken to trigger the prey escape response. This was defined as the difference between emergence from the refuge and point at which the prey initiated its escape response (trigger point). The predator's performance against the robot-controlled prey item was also assessed by recording the time taken to capture prey, which was defined as the time difference between the moment the prey initiated its escape response and the point at which the predator made physical contact with the prey.

R version 3.5.1 was used to calculate all predator and prey movement variables from the raw positional data, including the linear speed, acceleration and heading of the predator (R Development Core Team, 2019). Since spurious changes in heading might result from tracking error when the predator is stationary, heading angles were only calculated when the predator had moved a distance of 0.5 cm between frames. Data on predator and prey trajectories were combined to calculate the distance between the predator and the prey in each video frame, as well as the predator's bearing to the prey, which was defined as the absolute angular difference between the predator's heading and the line-of-sight between the predator and the prey (the straight line connecting the positions of the predator and the prey). Throughout the analysis, the prey escape angle was defined relative to the approaching predator, ranging from approximately 45° to 180°, with 180° indicating that the prey had escaped directly away from the predator. As the actual escape angle of the prey sometimes deviated slightly from the programmed escape path, all statistical analyses were based on realised escape angles, calculated from the known starting and end points of the prey's escape trajectory. Additionally, although the prey was programmed to respond when the predator had approached within 27 cm, the actual predator-prey distance at which the prey initiated its escape response (reaction distance) varied from trial to trial. This variability resulted from a combination of a short delay between the predator being detected and the initial movement of the prey, and differences in predator approach speeds across trials. The reaction distance was therefore defined as the distance between the predator and prey positions in the video frame immediately before the escape response was initiated. Prior to calculation of these variables, the prey trajectories were also smoothed with a Savitzky-Golay filter using a cubic fit and a filter length of 0.5 seconds in the signal R package (version: 0.7.6), to remove noise originating from manual extraction of the coordinates.

In the period immediately before the prey escape response was triggered (the *approach phase*), predators tended to accelerate in a straight line towards prey. As the prey was stationary during this period, the only information available to the predator about the prey's subsequent escape angle was from its experience of previous trials. The predator's maximum approach speed in each trial was therefore calculated to provide an indication of how predator behaviour was influenced by its experience of prey predictability during previous interactions. To obtain reliable estimates of maximum approach speeds, raw speed values from each trial were smoothed over time to reduce noise using LOESS (locally weighted regression). LOESS fits a smooth polynomial curve to the raw data by calculating the slope of a local regression line at multiple points along a time series. At each point, a set number of observations (determined by the span value) is considered when calculating the local slope. To ensure consistency between trials, the same span value of 0.1 was used throughout the analysis. This value was initially chosen by visually comparing plots of raw speeds with smoothed speeds, and selecting the span which reduced noise whilst also closely matching the original unsmoothed time series. To avoid generating a smoothed time series which includes negative values, which were sometimes produced when using LOESS to smooth data on the original scale, the raw speed values were log(x+1) transformed prior to smoothing. Adding a constant (+1) before log-transforming the data prevented undefined values from being generated as a result of the small number of instances when a fish was stationary and the raw speed was zero. Smoothed speeds on the original scale were then obtained by applying the inverse of this transformation, resulting in positive smoothed speed values, allowing the maximum approach speed in each trial to be calculated from the back-transformed smoothed speeds. The maximum predator approach speed was defined as the highest speed during the period in which the predator headed continuously towards the prey (i.e. the predator’s bearing to the prey did not exceed 45°), and did not subsequently deviate from this overall direction by heading away from the target. Speeds up to a limit of 10 seconds before the prey escape response was triggered were considered. Data from trials when predators triggered the prey escape response while approaching at a bearing of greater than 45° to the prey were not included in the analysis, as these trials are likely to reflect instances where the prey escape response was triggered inadvertently. To check the validity of this approach to calculating the maximum approach speeds, the maximum approach speeds obtained after applying LOESS to the log(x+1) transformed speed values were compared to the maximum approach speed values produced after applying LOESS to the untransformed data. There was a linear relationship between these two alternate measures, indicating that applying LOESS to the transformed data does not introduce any unintended biases (e.g. at high speed values), whilst also providing a good fit to the overall speed time series.

To quantify the predator's turning performance during the *pursuit phase* (the period after the prey escape response was triggered), both the predator's maximum turn speed and minimum turn radius were calculated, providing an indication of how rapidly and how sharply the fish turned during the pursuit (Combes *et al.*, 2012). Turn speed was defined as the change in the direction of the predator's heading in successive frames, and turn radius was calculated as the straight-line distance between the predator's position in frames i and $i+2$, divided by two times the sine of the change in the predator's heading θ between successive frames, i and $i+1$ (below, x and y indicate the x- and y-coordinates of the fish):

$$turn\ radius_i = \frac{\sqrt{(x_{i+2}-x_i)^2+(y_{i+2}-y_i)^2}}{2\sin(\theta_i)} \tag{1}$$

5.3.7 Statistical analysis

R version 3.5.1 was used to conduct all statistical analyses (R Development Core Team, 2019). Both linear mixed effects models (LMMs) and generalised linear mixed effects models (GLMMs) were used to explore the impact of various explanatory variables on the behaviour of predators before and after the prey initiated its escape response (i.e. both in the approach and pursuit phases). Whereas LMMs were fitted with lme4 package, GLMMs were fitted with the glmmTMB package. Random intercepts for individual identity were included in both types of model (details of any changes to this basic random effects structure in specific models are given below). Generalised additive mixed effects models (GAMMs), fitted using the mgcv package in R (version: 1.8.28), were also used to analyse time series of predator behaviour during the pursuit phase, as exploratory data visualisation revealed a possible non-linear relationship between the response and explanatory variables.

During parts of the analysis involving LMMs and GLMMs, the relative influence of explanatory variables on a given response variable was assessed by using AICc (Akaike's Information Criterion corrected for small sample sizes) values to compare the level of support from the data for a particular model, within a set of candidate models. AICc reflects a balance between how closely the model fits the data and overall model complexity (the number of estimated parameters in each model), with an additional penalty for small sample sizes (Burnham and Anderson, 2002). For each response variable analysed, most of the candidate models included within the model comparison set were formulated to test specific hypotheses about predator behaviour (**Table 5.1**). Additional models were also included within the comparison set to examine the effect of variables which were found be important at an early stage of the analysis (e.g. models featuring maximum predator approach speed), and to test the effect of specific interaction terms. For example, if one of the candidate models featured a two-way interaction term between two explanatory variables, a model including both main effects without the interaction term was also included, in order to provide a valid comparison for the additional effect of the interaction. To limit the number of candidate models being compared and therefore reduce the likelihood of generating false positives, simpler versions of three-way interaction models were not included in the initial model comparison set (Burnham and Anderson, 2002; Harrison *et al*., 2018). Models lacking the three-way interaction but retaining the constituent two-way interactions were only considered if the initial model comparison revealed that three-way interaction had an important effect.

Table 5.1: Models constructed to test hypotheses about predator behaviour in the approach and pursuit phases. The table shows which explanatory variables were included in models in order to test specific hypotheses. Additional explanatory variables were sometimes included to statistically control for the effects of confounding variables.

Predator behaviour during the approach phase	
Hypothesis	**Explanatory variables included in model**
Predators' approach behaviour changes over successive encounters (an improvement in the performance of the predator would be indicative of learning)	Trial number
Change in predators' approach behaviour over successive encounters is dependent on the predictability of the prey escape angle (if prey predictability affects the predators' ability to learn, the slope of the trial number effect should be more pronounced in the predictable treatment)	Trial number x Treatment
Change in predators' approach behaviour over successive trials is dependent on predictability of prey escape, but this effect is also influenced by the prey escape angle	Trial number x Treatment x Prey escape angle
Prey escape angle influences how predators approach prey, but only in the predictable treatment, in which uncertainty about the prey's likely escape direction is reduced	Treatment x Prey escape angle
Predator behaviour during the pursuit phase	
Predator pursuit behaviour of prey changes over successive encounters	Trial number
Change in predators' pursuit behaviour over successive encounters is dependent on predictability of prey escape	Trial number x Treatment
Tests whether maximum predator approach speed influences predator behaviour during the pursuit phase	Maximum predator approach speed
Tests whether the effect of maximum predator approach speed on predators' pursuit behaviour is dependent on the predictability of the prey escape angle	Treatment x Maximum predator approach speed
Variation in the prey's escape angle affects predator behaviour during the pursuit phase	Prey escape angle

At several stages of the analysis, it was important to account for the effects of confounding variables. When this was necessary, additional explanatory variables were added to all models within a model comparison set. In these circumstances, an additional model featuring just the relevant confounding variables was also included in the model comparison set to serve as the baseline for comparison with the other models. Reaction distance was included in several models to control for the potential impact of proximity to the prey at the point when the prey response was triggered. This variable was added to models constructed to analyse variation in the time taken to capture prey, the distance between the predator and the prey (over the course of the pursuit phase) and the speed and acceleration of the predator during the pursuit phase. Additionally, the predator's maximum approach speed was also included as an explanatory variable in models analysing the predator's speed or acceleration in the pursuit phase. This variable was included in order to control for the expected effect of approach speeds on pursuit speed or acceleration. In all model comparisons, a null model lacking any explanatory variables was also included, enabling all candidate models to be compared with a model lacking any predictive capacity. Within each comparison set, all models shared the same random effects structure.

When analysing variation in maximum predator approach speed and the time taken to capture prey, individual-level random slopes for the effect of trial number were also included within models, allowing the effect of trial number to vary between individual predators. In this context, models lacking random slopes would constrain individuals to share the same slope for trial number. Forcing all individuals to share the same slope has been shown to increase the chances of incorrectly concluding that interactions, such as the treatment x trial number interaction, have an important effect (Schielzeth and Forstmeier, 2009). Although it has been argued that random slopes should be included for each explanatory variable in the model to reduce false positive rates (Barr *et al*., 2013), there was insufficient data to fit the maximal random effects structure in each model (Harrison *et al*., 2018). Therefore, only random slopes for trial number were included in these models, as this relates directly to the central hypothesis being tested in the experiment (**Table 5.1**). Additionally, as there was sufficient data to do so, random intercepts for training group were also included in models with maximum predator approach speed and the time taken to capture prey as the response variable, to control for a lack of independence resulting from similar experiences during the training phase (individuals were nested within training groups). To aid model fitting, continuous explanatory variables were also scaled prior to being included in the model, by subtracting the mean and dividing by the standard deviation. Model assumptions were checked by examining QQ-plots of the residuals, residuals plotted against fitted values and by visualising the distribution of the conditional modes of the random intercepts. The DHARMa package (version: 0.2.7) was used to check model assumptions for GLMMs (Hartig, 2020). Variance inflation factors were also calculated to determine whether models were affected by collinearity between explanatory variables (Zuur, Ieno and Elphick, 2010).

To investigate how the pursuit strategy of fish changed over time within each trial, generalised additive mixed-effects models (GAMMs) were used to examine the impact of prey predictability and maximum predator approach speed on the predator's bearing to the prey over the course of the pursuit phase (defined as the angular difference between the predator's heading and the predator-prey line-of-sight as a response variable). GAMMs allow the relationship between the response and explanatory variables to be described by non-linear smooth functions, but guard against fitting overly complex smooth terms by using a penalised log-likelihood, in which penalty terms reflecting how quickly smooth functions change across their range are subtracted from the model log-likelihood (Pedersen *et al*., 2019). AIC scores were used to compare the fit of models containing different explanatory variables, starting with a baseline model including a linear term for the proportion of the pursuit phase completed. This variable was used instead of absolute time from the trigger point in order to standardise by pursuit duration. The existence of a non-linear relationship between the predator's bearing to prey and the proportion of the pursuit phase completed was verified by comparing the baseline model to a model including a smooth term for the proportion of the pursuit phase completed. Other models included in the comparison set featured interactions between the proportion of the pursuit phase completed and treatment or maximum predator approach speed, and controlled for the prey escape angle by including this variable as an additional smooth term. Random intercepts for individual identity and trial ID (nested within each individual) were also included in each model to account for non-independence in the observations. Model assumptions were verified by checking QQ-plots of model residuals and plots of model residuals against fitted values. Model residuals were also checked for temporal auto-correlation by examining complete and partial auto-correlation function plots.

Inter-individual variation in the time taken to leave the refuge and in the maximum approach speed of the predator was also quantified by estimating adjusted repeatabilities with the rptR package (version: 0.9.22) in R (Stoffel, Nakagawa and Schielzeth, 2017). This approach to evaluating inter-individual differences uses a mixed model framework, allowing explanatory variables to be controlled for through their inclusion as fixed effects (Nakagawa and Schielzeth, 2010). The time taken to leave the refuge was modelled using a Poisson GLMM, with standard body length, trial number, treatment and the treatment x trial number interaction included as fixed effects. The treatment x trial number interaction was included in the model to account for the possibility that fish in the unpredictable treatment might progressively lose motivation over the course of the experiment. Maximum predator approach speed was modelled with an LMM, which included the interaction between treatment and prey escape angle, trial number, standard body length and the time taken to trigger the prey escape response as explanatory variables. Both models shared the same random effects structure, which included random intercepts for training group identity and random slopes for the effect of trial number on individuals (individuals were nested within training groups). Statistically significant repeatability estimates were those for which the 95% confidence intervals (obtained via parametric bootstrapping) did not overlap with zero. The magnitude of inter-individual differences in the effect of trial number on maximum predator approach speed was also assessed by comparing the conditional AIC (cAIC) of the LMM described above to an otherwise identical model lacking individual-level random slopes for the effect of trial number, using the cAIC4 package in R (version: 0.9; Säfken *et al.*, 2018). Like AICc, cAIC provides a metric of the relative fit of a model by reflecting the balance between model fit and model complexity, but cAIC can also be used to compare two otherwise identical models which differ in their random effects structure (Greven and Kneib, 2014).

5.3.8 Simulations of predator pursuit strategies

Simulations of predator pursuit strategies were also conducted to explore the consequences of prey predictability on the predator's ability to track and intercept its target. Pure pursuit and parallel navigation are two possible pursuit strategies employed by predators to track a moving target (Fabian *et al*., 2018). These two strategies differ in how the predator steers in relation to the target: when following a pure pursuit strategy, predators adjust their heading so that it remains aligned with the line-of-sight to the prey, whereas in parallel navigation the predator steers to maintain a constant line-of-sight angle, allowing the predator to eventually intercept its target (Brighton, Thomas and Taylor, 2017; McHenry *et al*., 2019). Pursuit strategies can be distinguished by analysing predator trajectories featuring a substantial degree of turning, in which the prey is actively escaping. As only trials where the predator is forced to manoeuvre are informative (Brighton, Thomas and Taylor, 2017), the analysis of pursuit trajectories was therefore restricted to data from trials where the prey escaped at an acute angle (< 90°). From these trials, trajectory data from the moment when the prey started moving along its escape trajectory (trigger point) until the instant the prey had stopped moving and completed the escape response were analysed. In this analysis, each video frame corresponds to a separate observation.

The pursuit strategy of the predators was tested by comparing the measured trajectories of fish in each experimental trial to simulated trajectories based on either pure pursuit or parallel navigation. In this approach, based on methodology outlined by McHenry *et al*. (2019), a proportional pursuit guidance law was used to describe how the predator changes its heading in response to the movement of prey. At each time-step in the simulation, the following differential equation was used to model changes in the heading of the predator:

$$\dot{\theta} = k \sin(\alpha_t + \varphi_t - \theta_t) \tag{2}$$

In the above equation, θ_t is the predator's heading at the current time t, k represents the proportional gain constant (k > 0) determining the magnitude of the change in heading resulting from a given input and α_t is the predator-prey line-of-sight angle at time t (see **Fig. 5.4**). φ_t represents the bearing set-point, which is calculated differently depending on whether a pure pursuit or parallel navigation strategy is simulated. In simulations based on a pure pursuit strategy, φ_t was held constant at zero throughout the entire pursuit. This corresponds to a pursuit in which the predator steers to remain aligned with the angle of the line-of-sight to prey. Following the approach set out by McHenry *et al*. (2019), for parallel navigation φ_t was allowed to vary over the course of the pursuit, according to the following equation:

$$\varphi_t = \sin^{-1}\left(\frac{\sin\beta_t}{V_t}\right) \tag{3}$$

In the equation 3, β_t indicates the heading of the prey relative to the line-of-sight angle, α_t, in the current time-step (**Fig. 5.4**). At time points in the pursuit when the predator was travelling at a greater speed than the prey, V_t was defined as the measured speed of the predator divided by the speed of the prey. When the speed of the predator dropped below that of the prey, V_t was set to equal one to avoid undefined values of φ_t being produced.

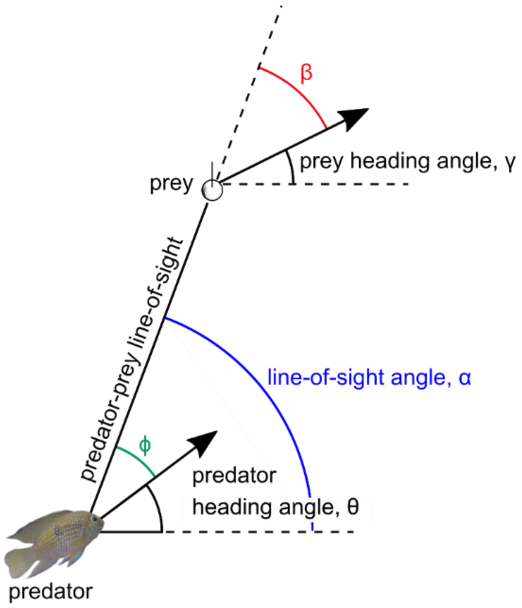


Figure 5.4: Diagram illustrating definitions of angles used in simulations of predator pursuit trajectories. Predator and prey heading angles, and the predator-prey line-of-sight angle, are defined relative to an external frame of reference marked by the dashed horizontal line. This was arbitrarily chosen but remained the same for all trials throughout the analysis.

At each time-step in the simulation, a solution to equation (2) was found numerically using Euler's forward method, allowing the predator's heading in the next time-step to be calculated as follows:

$$\theta_{t+1} = \theta_t + h \cdot k \sin(\alpha_t + \varphi_t - \theta_t) \qquad (4)$$

Here, θ_{t+1} is the predator's heading in the next time-step t+1 and h is the time difference between time-steps in the simulation, which is equal to the gap between video frames (h = 0.04 seconds). Simulations were run from the time the prey started its escape response until the prey had stopped moving and completed its escape manoeuvre, with as many time-steps as the number of video frames required to cover the duration of the pursuit. Experimental measurements of the predator's heading and position at the trigger point were used as initial values at the start of each simulation. At each time-step, the simulated heading was used to calculate the predator's projected position, by combining the simulated heading with the displacement calculated from measured values of the predator’s speed during that particular frame. Using measured speed values to calculate the displacement of the predator at each time step ensures that any differences between the observed and simulated trajectories can be attributed to the accuracy with which either strategy predicts directional changes during the pursuit (McHenry *et al*., 2019).

The degree to which the simulations reproduced the observed trajectories was assessed by calculating the mean distance between the actual and simulated positions of the predator at all time-steps over the course of the pursuit. The resulting mean error indicates the extent to which predators followed a trajectory predicted by pure pursuit or parallel navigation in each trial. For both pure pursuit and parallel navigation, the optimal value of k (see equations 1 and 3) was chosen by conducting independent simulations over a range of possible k values (increasing from 0.05 to 10 in 0.05 increments) and selecting the value which minimised the mean error in each trial. Once the best-fitting values of k had been found, the proportion of each pursuit that could be predicted accurately by pure pursuit or parallel navigation was calculated, across a range of pre-specified error thresholds. In order to account for variation in the distance travelled in each pursuit, error threshold values used were expressed as a proportion of the total length of the pursuit trajectory, and ranged from 1 to 10%. Similar to the approach used in two recent studies (Brighton, Thomas and Taylor, 2017; McHenry *et al*., 2019), this involved running a series of simulations of varying lengths. As the duration of each pursuit varied from trial to trial, all simulations started at the point in time when the prey started moving, but the end-point varied, ranging from 0.2 seconds after the trigger point and increasing at 0.04 second intervals until the time when the prey stopped moving. For each trial, the proportion of each pursuit accurately predicted by pure pursuit or parallel navigation was obtained by finding the longest simulation producing an overall mean error of less than the threshold. GLMMs featuring the mean error as a response variable were also used to determine the effect of treatment and the predator’s maximum approach speed on the extent to which predators followed or deviated from a pure pursuit strategy.

To confirm the results of the simulations described above, the correlation between the predator-prey line-of-sight angle and the heading angle of the predator was also estimated. This was achieved by calculating median of the Kendall's tau correlation coefficients (τ) for circular data across all the trials, using the BAMBI R package (version: 2.2.0). Kendall's tau is a non-parametric test which takes the inherent periodicity of data measured as angles into account (Zhan *et al*. 2017). Possible time delays in the predators' ability to track the movement of prey were also explored by computing the lagged circular correlation between the predator's heading and the line-of-sight angle. For each trial, correlation tests were repeated across a range of time offsets for the line-of-sight angle, increasing from zero at 0.04 second intervals up to point when the prey stopped moving. The median time lag across all the trials which maximised τ was reported.

5.4 Results

5.4.1 Performance of the robotic prey system

During the test phase of the experiment, blue acara cichlids left the refuge in 532 out of a total of 540 trials. The prey escape response was triggered in 524 of the 532 trials in which the predator emerged from the refuge. Although the time taken for the predator to leave the refuge was not significantly repeatable between individual fish during initial boldness tests (R = 0.1, 95% confidence intervals: 0 - 0.443, P = 0.286), the time taken to leave the refuge was significantly repeatable in test phase trials (R = 0.383, 95% confidence intervals: 0.176 - 0.454, P < 0.001). Additionally, individual predators consistently differed in the time taken to trigger the prey escape response (R = 0.332, 95% confidence intervals: 0.191 – 0.482, P < 0.001). Out of the 524 trials in which fish left the refuge, the prey travelled along the full length of its programmed escape path in 519 trials; in the 5 trials where the escape response ended prematurely, the loss of the magnetic connection between robot and the prey is likely to have been the cause.

Throughout the experiment, the prey escape angle was defined relative to the approaching predator, but the programmed prey escape angles did not always perfectly match the angle of the actual prey trajectory: the median angular difference between the expected and realised prey escape angle was 8.5° (inter-quartile range, IQR = 10.7°). Based on a comparison of model AICc values, with a difference of greater than two units indicating strong support for one model over another (Burnham and Anderson, 2002), there were no substantial systematic differences in the directional error of the robotic prey system between the predictable and unpredictable treatments (**Table 5.2**). Additionally, there was no association between the expected prey escape angle and the angular difference between the expected and realised prey escape angles (**Table 5.2**), indicating that the directional error in the robotic prey system did not vary systematically with the prey's escape angle.

Table 5.2: Results of Gamma GLMs (generalised linear models) explaining variation in the angular difference between expected and realised prey escape angles and LMMs (linear mixed-effects models) explaining variation in reaction distance. LMMs were used when analysing reaction distances to allow random effects for individual fish identity to be included (controlling for a lack of independence produced by analysis repeated measures of individual predator) because reaction distance is likely to be influenced by the speed of the attacking predator.

Response variable	Explanatory variables	Degrees of freedom	AICc	ΔAICc
Angular difference between expected and realised escape angles	Treatment	3	3773.6	0.00
	Null model (no explanatory variables)	2	3775.6	1.97
	Expected escape angle	3	3776.2	2.62
Reaction distance	Null model (no explanatory variables)	3	2281.3	0.00
	Treatment	4	2282.0	0.73

In most trials (381 out of 519), the escaping prey elicited a rapid pursuit by the predator which culminated in the prey item being consumed, and in many instances (214 out of 381 trials), the predator captured the prey item before the prey had completed its programmed escape trajectory. In order to focus on trials in which the predator was fully motivated to attack and pursue prey in the lead-up to an attack, the analysis was limited to the subset of 364 trials in which the predator approached the prey directly (i.e. at the time when the prey escape response was triggered, the bearing of the predator to the prey was less than 45°) and subsequently made contact with the prey. Due to a combination of a short delay between the predator being detected and the initial movement of the prey, and differences in predator approach speeds across trials, the actual predator-prey distance at which the prey initiated its escape response (reaction distance) varied from trial to trial. However, there was no overall difference in reaction distance between the two treatments (**Table 5.2**).

5.4.2 Predator behaviour during the approach phase

To investigate whether predators adjusted their behaviour in response to the prey escape strategy they encountered over successive trials, I compared a set of models predicting the maximum speed of the predator during the approach phase (i.e. the period before the prey escape response was triggered). During this period, the only information available to the predator about the prey's likely escape direction was from its experience of escape responses during previous trials. By approaching prey rapidly, predators can reduce the distance to the prey at the time the prey reacts, lowering the probability of a successful escape response (Walker *et al*., 2005), but a rapid approach can constrain the ability of the predator to accurately target prey (Higham, 2007). For prey, performing a sharp evasive turn when the predator is committed to an attack and is moving too quickly to adjust its trajectory might represent an effective escape strategy (Howland, 1974; Blaxter and Fuiman, 1990; Corcoran and Conner, 2016). Over multiple interactions, this raises the possibility that predators might learn to adjust their approach speed when relatively certain about the direction prey will escape in, in order to counter a potentially effective escape manoeuvre (Croy and Hughes, 1991; Reid, Seebacher and Ward, 2010).

The model including the interaction between treatment (unpredictable vs. predictable) and prey escape angle received most support from the data (**Table 5.3**). For predators which encountered predictable prey, the maximum speed attained during the approach phase was dependent on the prey's escape angle, but in the unpredictable treatment, no relationship between maximum approach speed and prey escape angle was observed (**Fig. 5.5**). In the predictable treatment, predators reached higher maximum speeds when approaching prey which were programmed to escape predictably directly away from them, and approached at lower speeds when attacking prey which escaped at an acute angle (<90°). In addition, a model featuring trial number as an explanatory variable also represented a substantial improvement in fit over the null model, as indicated by the AICc difference of greater than two units between this model and the null (**Table 5.3**). Trial number had a positive influence on the predator's maximum approach speed and trial number, but this relationship was not affected by the predictability of the prey's escape angle, as demonstrated by the relatively poor fit of a model featuring an interaction between treatment and trial number (**Table 5.3**). This suggests that the experimental treatment had no influence on the change in the predator's maximum approach speed over the full range of the experiment, from trial 1 to trial 20. Although there was no evidence that the effect of trial number on maximum approach speed was influenced by treatment (**Table 5.3**), the effect of trial number did vary considerably between individual predators (**Fig. 5.6**), as shown by the large reduction in model fit when individual-level random slopes for trial number were removed from the top-supported model (ΔcAIC: 66.7). Individual acaras also differed consistently in their average maximum approach speeds, as shown by the high adjusted repeatability of this variable, even when statistically accounting for both standard body length and the time taken to trigger the prey escape response during each trial ($R = 0.399$, 95% confidence intervals: 0.216 - 0.529, $P < 0.001$).

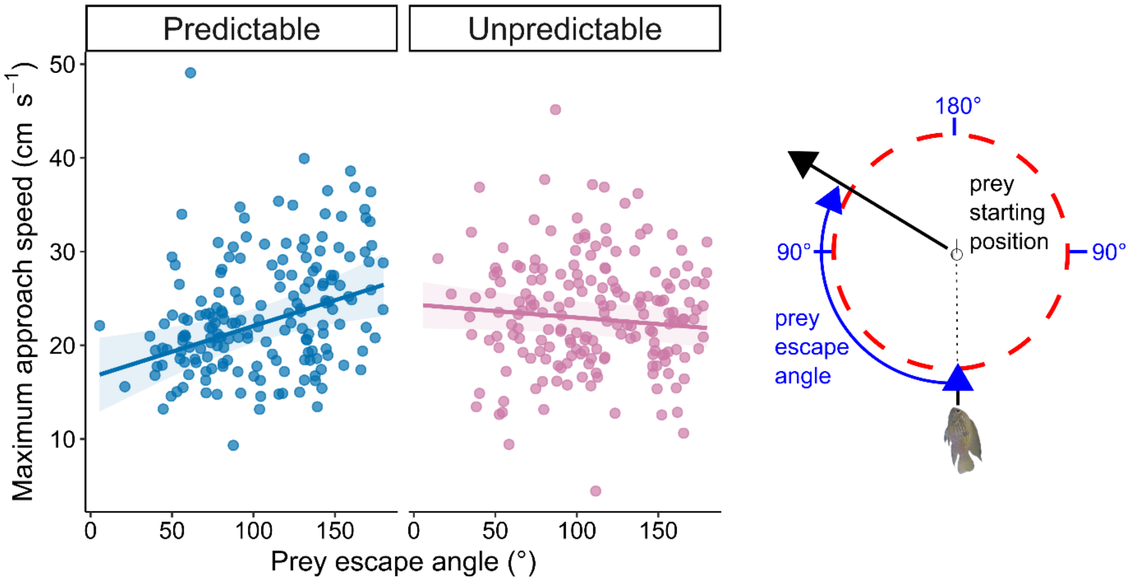


Figure 5.5: Influence of the interaction between treatment (predictable vs unpredictable) and prey escape angle on the maximum approach speed of the predator. The coloured lines indicate the predicted fit from the top-supported model in **Table 3**, with the shaded area representing the 95% confidence intervals surrounding the predicted values. Each data point represents a single trial.

Table 5.3: Results of LMMs (linear mixed-effects models) explaining variance in maximum speed of the predator during the approach phase, based on 364 observations of 25 individual fish. All LMMs included random intercepts for training group identity and random slopes for the effect of trial number on individuals (individuals were nested within training groups).

Explanatory variables	**Degrees of freedom**	**AICc**	**ΔAICc**
Treatment x Prey escape angle	9	2229.3	0.00
Trial number	7	2233.0	1.89
Treatment x Trial number x Prey escape angle	13	2233.4	4.08
Null model (no explanatory variables)	6	2234.2	4.88
Standard body length	7	2234.5	5.24
Treatment + Trial number	8	2234.9	5.60
Treatment x Trial number	9	2236.1	6.78
Prey escape angle	7	2236.2	6.98
Treatment + Prey escape angle	8	2238.0	8.74

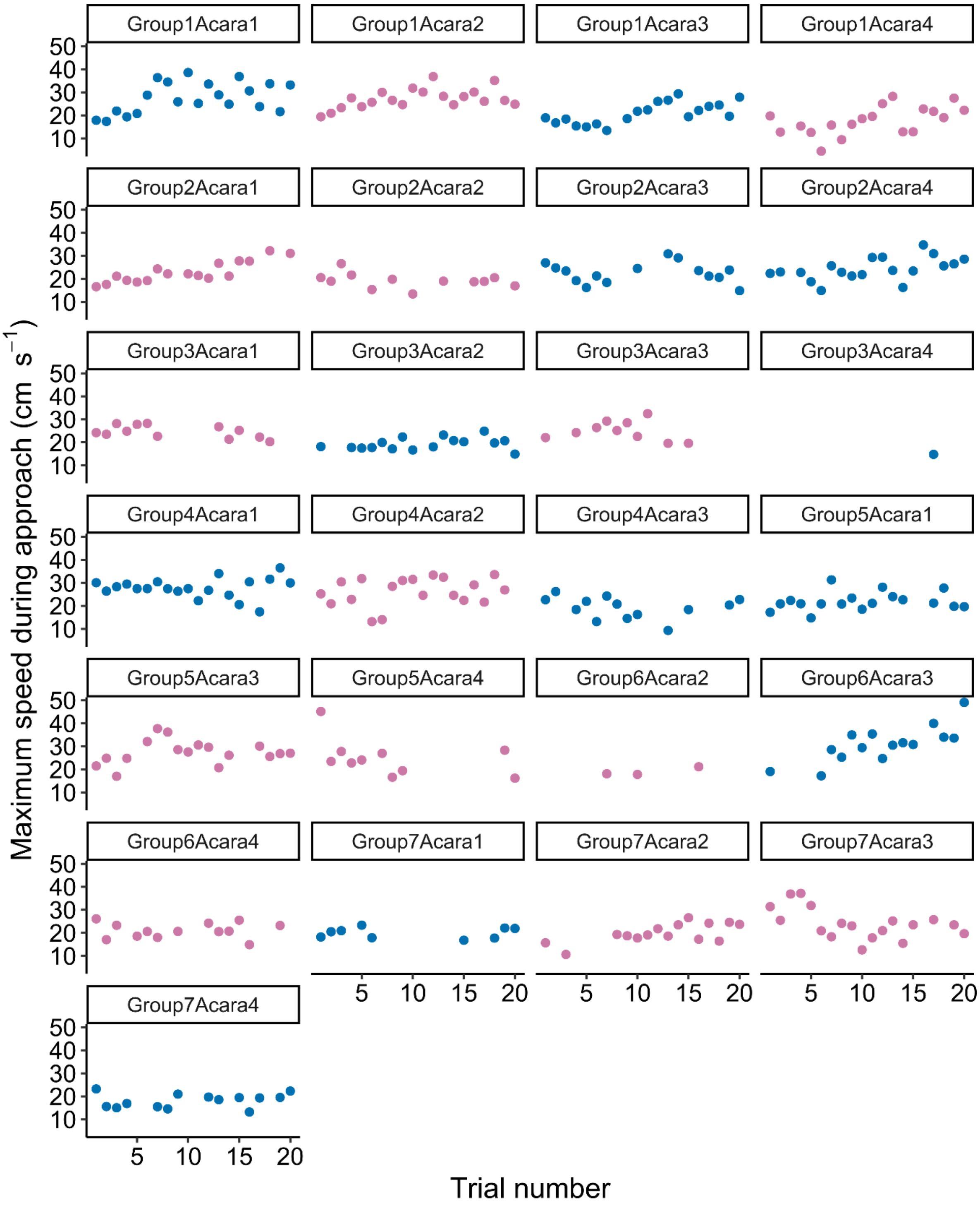


Figure 5.6: The relationship between maximum approach speed and trial number, for each individual predator tested in the experiment. Colours indicate which treatment an individual was assigned to (predictable: blue points; unpredictable: pink points).

In the predictable treatment, individual predators always experienced prey escaping at the same angle, leading to a potential confound between the prey's escape angle and individually-repeatable traits of each fish. The positive relationship between the predator's maximum approach speed and the prey's escape angle for predictable prey could therefore have been driven by inherent differences between individual predators in variables affecting the capacity to attain high speeds when approaching prey, such as body size or motivation, rather than reflecting behavioural adjustment to the prey's angle of escape. If this were the case, variation between individual predators would be a stronger predictor of approach speeds than the prey's escape angle. However, when compared to models including standard body length, the approach speed of the predator in the first trial or the time taken for the predator to trigger the prey escape response (an indicator of motivation), the model including prey escape angle was the only model to represent an improvement in fit over the null model (**Table 5.4**). This suggests that the relationship between maximum approach speed and prey escape angle in the predictable treatment was unlikely to have arisen due to inter-individual variation in speed, body size or motivation.

Table 5.4: Results of LMMs explaining variance in maximum speed of the predator during the approach phase, in the predictable treatment, based on 179 observations of 12 individual fish. All LMMs included random intercepts for training group identity and random slopes for the effect of trial number on individuals (individuals were nested within training groups).

Explanatory variables	**Degrees of freedom**	**AICc**	**ΔAICc**
Prey escape angle	7	1081.8	0.00
Prey escape angle x Trial number	9	1082.9	1.07
Maximum approach speed in first trial	7	1086.8	4.96
Time taken to trigger the prey escape response	7	1087.5	5.68
Trial number	7	1087.9	6.09
Null model (no explanatory variables)	6	1088.0	6.23
Standard body length	7	1088.8	6.95

5.4.3 Consequences of variation in maximum predator approach speed

A model comparison approach was also used to determine which factors influenced the time taken to capture prey. Since most approaches by the predator resulted in the prey being captured within less than 10 seconds, trials in which fish failed to capture prey within this time limit were not considered, as the predator was unlikely to be sufficiently motivated to pursue prey. By restricting the analysis to this subset of the data, 38 trials were excluded, leaving 326 observations of 23 individual fish. As it was important to control for the effect of variation in prey reaction times on these outcomes, all of the models that were constructed included the reaction distance as an explanatory variable.

Three models, all of which included the predator's maximum approach speed as an explanatory variable, had similar AICc scores, and represented a substantial improvement in model fit over the baseline model featuring only reaction distance (**Table 5.5**). The least complex model within this group included maximum predator approach speed and reaction distance as main effects, highlighting the presence of a strong negative relationship between the predator's maximum approach speed and the time taken to capture prey (**Fig. 5.7**). Although the model including maximum predator approach speed and reaction distance was the simplest, and therefore the most parsimonious, there was some tentative evidence to suggest that the prey's escape angle had a positive influence on the time taken to capture prey: among the three best-supported models, the model including main effects for these two variables had the lowest AICc score by a margin of 1.17 units (**Table 5.5**). However, the most complex model within this group, which included an interaction between maximum predator approach speed and prey escape angle, performed similarly (or marginally worse) than the model including only main effects for maximum predator approach speed and reaction distance, suggesting that the direction or strength of the negative relationship between approach speed and the time taken to capture prey was not dependent on the prey's escape angle. The remaining models tested did not result in an improvement in fit when compared to the baseline model featuring only reaction distance as an explanatory variable. Treatment, trial number or prey escape angle, or interactions involving these variables, were therefore not associated with variation in the time taken to capture prey. Even though the predator's maximum approach speed was influenced by an interaction between treatment and prey escape angle (**Fig. 5.5**), this association did not translate into an effect on the time taken to capture prey, as demonstrated by the poor performance of the model featuring treatment and prey escape angle compared to a model including these explanatory variables as main effects (**Table 5.6**).

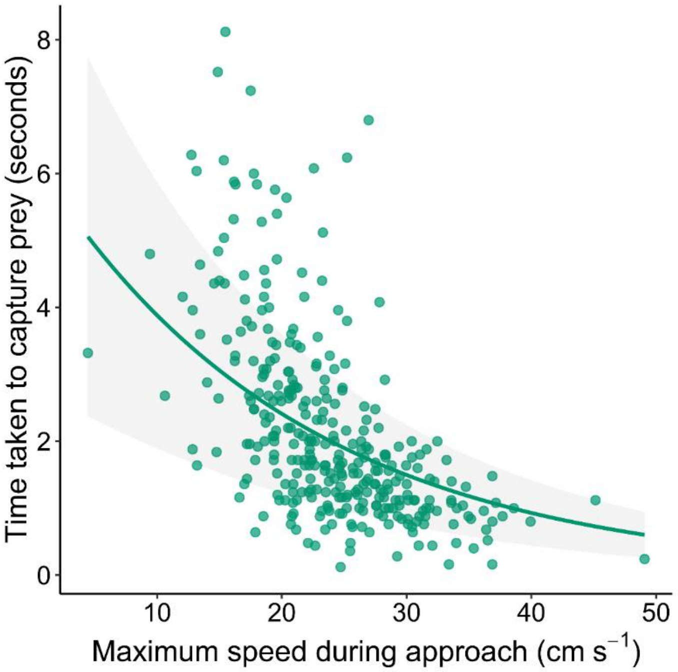


Figure 5.7: Effect of the maximum speed of the predator during the approach on the time taken to capture prey. The curve indicates the predicted fit from the top-supported model in **Table 5**, with the shaded area representing the 95% confidence intervals surrounding the model fit. Each data point represents a single trial.

Table 5.5: Results of Gamma GLMMs (generalised linear mixed-effects models) explaining variance in the time taken to capture prey, based on 326 observations of 23 individual fish. All GLMMs included random intercepts for training group identity and random slopes for the effect of trial number on individuals (individuals were nested within training groups).

Explanatory variables	**Degrees of freedom**	**AICc**	**ΔAICc**
Maximum predator approach speed + Prey escape angle + Reaction distance	9	785.8	0.00
Maximum predator approach speed + Reaction distance	8	787.0	1.17
Maximum predator approach speed x Prey escape angle + Reaction distance	10	787.6	1.83
Reaction distance	7	842.8	56.97
Prey escape angle + Reaction distance	8	842.8	56.97
Trial number + Reaction distance	8	844.9	59.07
Treatment + Prey escape angle + Reaction distance	9	844.9	59.07
Treatment x Prey escape angle + Reaction distance	10	846.6	60.79
Trial number + Treatment + Reaction distance	9	847.0	61.17
Treatment x Trial number + Reaction distance	10	848.0	62.16
Treatment x Trial x Prey Escape angle + Reaction distance	14	853.7	67.95
Null model (no explanatory variables)	6	931.5	145.67

5.4.4 Predator pursuit strategy

Despite the strong negative correlation between maximum predator approach speeds and the time taken to capture prey (**Fig. 5.7**), predators in the predictable treatment approached prey programmed to escape at an acute angle more slowly than prey escaping directly away from them (**Fig. 5.5**). Given that higher maximum predator approach speeds are associated with prey being captured more rapidly regardless of the prey's escape angle (**Table 5.5**), the advantage gained from a slower approach is unclear. One possible explanation is that fish adaptively reduced their approach speed when attacking prey which predictably escaped at acute angles. If there is a trade-off between speed and manoeuvrability, predators might have slowed down so that they were able to turn more effectively when pursuing prey which escaped at an acute angle (Domenici, 2001; Wilson *et al*., 2015). A reduction in approach speed might also have enabled predators to pursue predictable prey more efficiently by reducing the distance travelled, by turning to intercept their target. Greater efficiency might also be reflected in a reduction in the variability of the predators' speed and acceleration throughout the pursuit. To explore the implications of a slower approach in more detail, I considered data from the 116 trials in both treatments where prey escaped at an acute angle (< 90°), as this subset of the data should be most informative about the consequences of a reduction in approach speed in the predictable treatment.

By analysing the geometry of predator and prey trajectories during the pursuit phase, I first tested whether predators were pursuing prey by swimming directly towards their target (i.e. a pure pursuit strategy), or were instead attempting to intercept the prey by moving towards a point ahead of the prey's current position. In pure pursuit, the predator's heading is aligned with the line-of-sight between the predator and the prey (defined as the bearing of the straight line between the positions of the predator and the prey, **Fig. 5.8a**), which tends to result in a characteristic curved trajectory (Haselsteiner, Gilbert and Wang, 2014). In contrast, prey interception can be achieved through parallel navigation, in which the line-of-sight between the predator and the prey is maintained at a constant angle (Brighton, Thomas and Taylor, 2017). This strategy can be more efficient than a pure pursuit, particularly when prey follow a straight escape path (McHenry *et al*., 2019), and has previously been documented in predatory bats, insects and birds of prey (Ghose *et al*., 2006; Brighton, Thomas and Taylor, 2017; Fabian *et al*., 2018). In this experiment, experience of the prey's escape trajectory might enable predators to react to the prey's escape response more effectively by switching to a more efficient strategy resembling parallel navigation. The pursuit strategy adopted by the predator is also important to understand in relation to other aspects of pursuit performance, because it influences the degree of turning expected from the predator throughout the chase.

Predators captured the prey item before the prey had completed the entirety of its programmed trajectory in 75 of the 116 trials in which the prey escaped at an acute angle. On average there was a strong positive correlation between the line-of-sight angle and the angle of the predator’s heading (median Kendall’s circular rank correlation coefficient across trials: $\tau = 0.79$, IQR = 0.22, **Fig. 5.8b**) during the period of the pursuit when the prey was actively escaping (i.e. had not yet reached the end of the escape path). This suggests that the fish were following a pure pursuit strategy (Brighton and Taylor, 2019), and in many of the trials the predator-prey line-of-sight angle was not held constant throughout the pursuit, in a manner which is inconsistent with parallel navigation (**Fig. 5.8c**). The correlation between the line-of-sight angle and the predator’s heading peaked at a median time delay of 0.04 seconds (IQR: 0.16), which did not differ between the predictable and unpredictable treatments (predictable: 0.04 seconds, IQR: 0.12; unpredictable: 0.04 seconds, IQR: 0.19), suggesting that the experimental treatment did not influence the speed with which predators adjusted their heading to track the movement of prey. Results from simulations were also consistent with predators following a pure pursuit strategy when tracking escaping prey. For mean error thresholds under 5%, a pure pursuit model predicted a greater proportion of the predator’s pursuit trajectory than a model based on parallel navigation (**Fig. 5.9a**). Whereas the pure pursuit model closely matched the observed trajectories in most trials, parallel navigation was often a poor fit to the experimental data (**Fig. 5.9b**). When comparing the predictable and unpredictable treatments, there was also no overall difference in the overall mean error between the measured trajectories and simulations based on pure pursuit (**Fig. 5.10a, Table 5.6**), indicating that the experimental treatment did not influence the degree to which predators followed a pure pursuit strategy when chasing the prey. While there was evidence for a positive relationship between the mean error for pure pursuit and trial number, no relationship was found between the mean error and the maximum approach speed of the predator (**Fig. 5.10b, Table 6**).

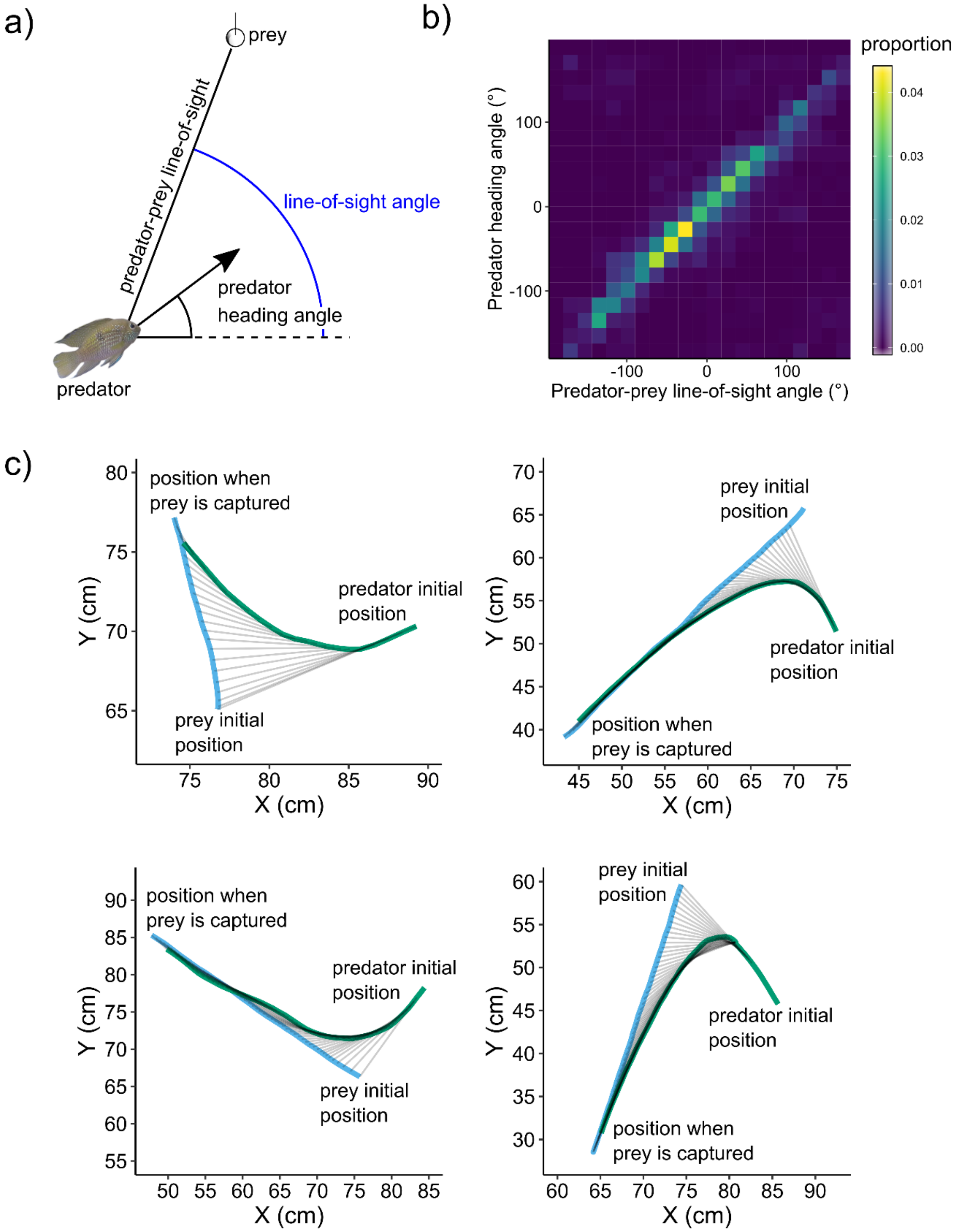


Figure 5.8: Predator and prey trajectories during the pursuit phase. (a) Diagram illustrating definitions for the predator heading angle relative to an external frame of reference and the line-of-sight angle between the predator's position to the prey and an external frame of reference. The black arrow indicates the direction the predator is moving in, and the dashed line indicates the

external frame of reference used to measure angles across all trials. (b) Correlation between the predator-prey line-of-sight angle and predator heading angle in trials in which the prey escaped at an acute angle. The positive relationship indicates that the trajectory of the acaras follows a pure pursuit course (from the moment the prey initiated its escape response until prey capture). Colours indicate the proportion of total observations falling within a set interval. Observations correspond to the angles recorded at 0.04 time-points within each trajectory pooled across all trials in which the prey escaped at an acute angle. (c) Characteristic trajectories for the predator (green) pursuing the prey (blue), shown from the point when the prey initiated its escape response until prey capture and highlighting the line-of-sight angle (grey lines). Labels indicate the initial position of both the predator and the prey at the moment the prey started moving, and their positions when the predator captured the prey. The predator-prey line-of-sight angle does not remain constant over the course of the pursuit, suggesting that predators are not using parallel navigation to intercept prey.

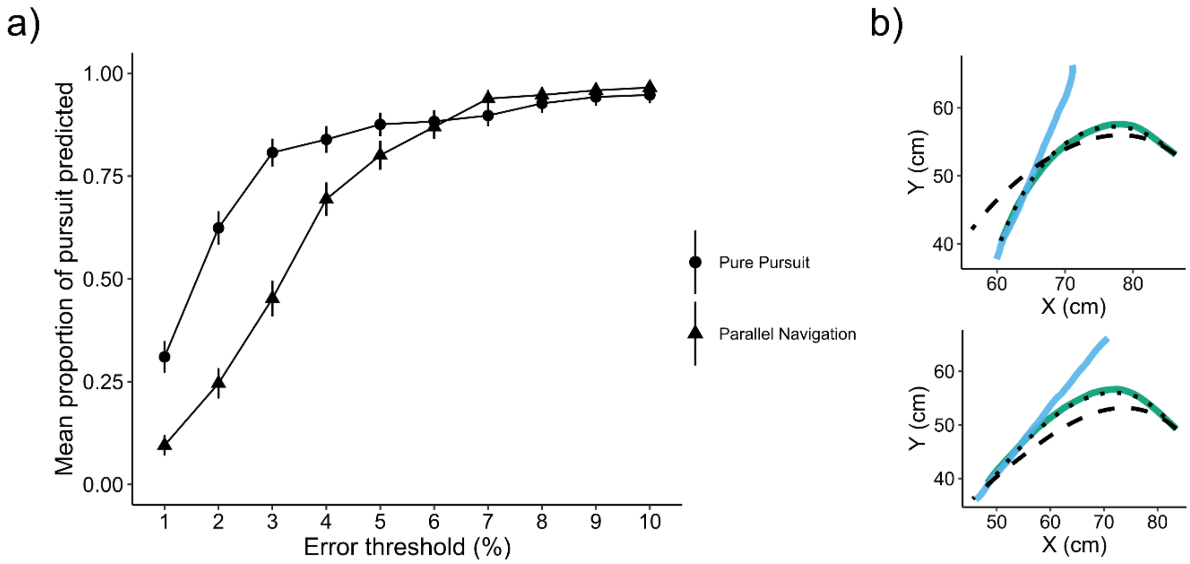


Figure 5.9: A comparison between the observed pursuit trajectory of predators and simulated trajectories based on models of pure pursuit and parallel navigation. (a) Mean proportion of the period of the pursuit when the prey was moving predicted by pure pursuit (circles) or parallel navigation (triangles), across a range of error threshold values. Error bars indicate standard errors. (b) Examples of illustrative trajectories from two trials showing the close match between the simulated pure pursuit trajectories (dotted black line) and the observed path of the predator (dark green curve), and the relatively poor fit of simulated trajectories based on a parallel navigation strategy (dashed black line). The trajectory of the prey is shown in blue, and prey capture occurs where the paths converge.

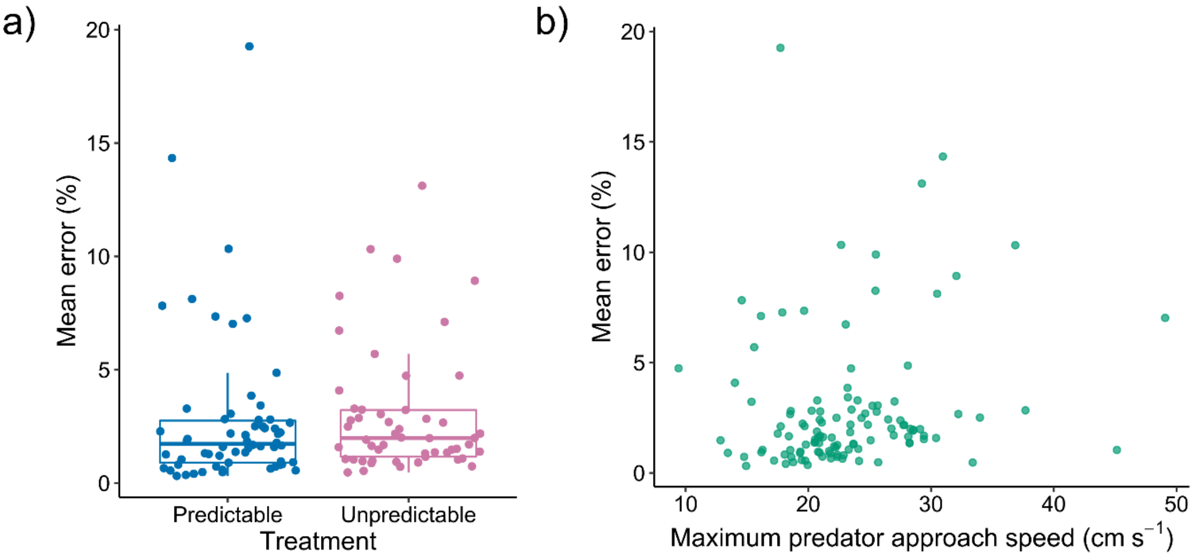
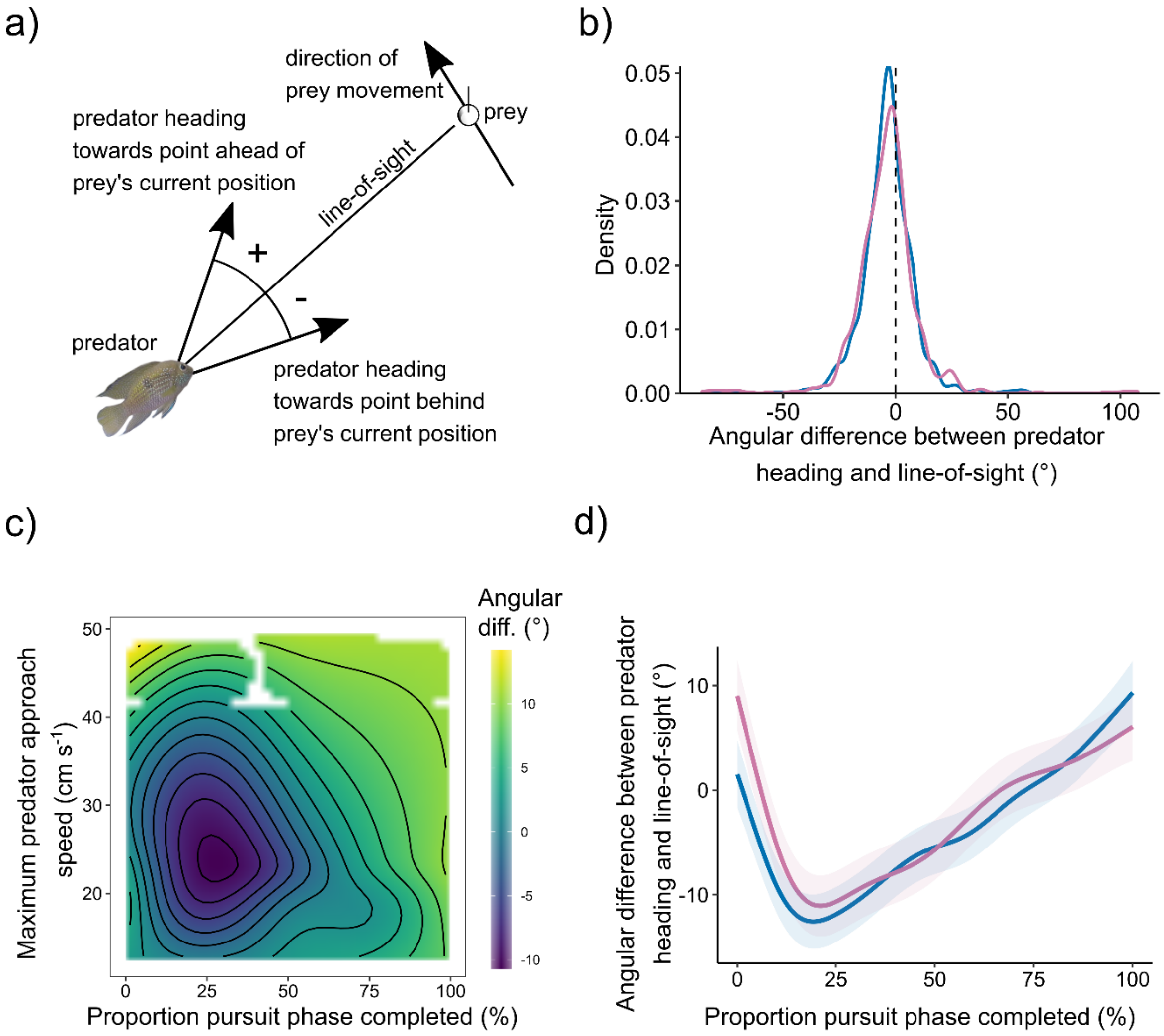


Figure 5.10: The relationship between (a) treatment (predictable vs. unpredictable) or (b) maximum predator approach speed and the mean percentage error in the observed pursuit trajectory of the predator, relative to simulations of a pure pursuit strategy. Data points correspond to a single trial.

Table 5.6: Results of Gamma GLMMs predicting the mean percentage error in the observed pursuit trajectory of the predator, relative to simulations of a pure pursuit strategy, based on 116 observations of 19 individual fish in trials where prey escaped at an acute angle (< 90°).

Explanatory variables	**Degrees of freedom**	**AICc**	**ΔAICc**
Treatment x Trial number + Prey escape angle + Reaction distance	8	438.1	0.00
Trial number + Prey escape angle + Reaction distance	6	438.1	0.00
Treatment + Trial number + Prey escape angle + Reaction distance	7	440.4	2.26
Prey escape angle + Reaction distance	5	440.6	2.47
Maximum predator approach speed + Prey escape angle + Reaction distance	6	441.8	3.70
Treatment + Prey escape angle + Reaction distance	6	442.6	4.45
Maximum predator approach speed x Treatment + Prey escape angle + Reaction distance	8	443.1	5.01
Maximum predator approach speed + Treatment + Prey escape angle + Reaction distance	7	443.9	5.82
Null model (no explanatory variables)	3	465.6	27.53

Although the overall geometry of the observed trajectories indicates that the acaras were following a pure pursuit strategy, the heading of the fish was not always closely aligned with the angle of the line-of-sight to prey throughout the pursuit phase. Given that the prey's escape path was approximately straight, a lack of alignment at any given instant could indicate that the predator is either heading towards a point ahead of, or heading towards a point behind, the prey's current position (**Fig. 5.11a**). The distribution of the predators' bearings to prey peaked close to zero (indicating alignment between the predator's heading and the line-of-sight), but also showed considerable variation either side of this point (**Fig. 5.11b**). Over the course of the pursuit, changes in the predator's bearing to prey depended on the predator's maximum approach speed, as demonstrated by the fact that the model receiving most support from the data featured an interaction between non-linear smooth terms for approach speed and the proportion of the pursuit completed (**Table 5.7**). This model represented an improvement in fit over a model featuring non-interacting smooth terms for these two explanatory variables, as well as a model including only a smooth term for the proportion of the pursuit completed. Inspection of the interaction surface generated by the top-supported model indicated that predators which approached prey at intermediate speeds (the median maximum approach speed was 22.4 cm s^{-1}) initially moved directly towards the prey, but started to head towards a point behind the prey's current position as the pursuit progressed (**Fig. 5.11c**). Then, after reaching a minimum at approximately 25% through the pursuit, the bearing to prey gradually increased until the predator was heading directly towards or marginally ahead of the prey's current position at the point of capture. In contrast, the movements of predators which approached prey at lower speeds remained more closely aligned to prey throughout the pursuit, or ahead of prey throughout the pursuit for predators which approached prey more rapidly (**Fig. 5.11c**). Additionally, a model including an interaction between treatment and the proportion of the pursuit completed received more support than the model which included non-interacting effects of treatment and the proportion of pursuit completed (**Table 5.7**). While this suggests that the change in the predators' bearing to prey was influenced by prey predictability, the largely overlapping 95% confidence intervals surrounding the predicted curves for the two treatments indicates that the differences between them are likely to result from slight changes in the shape of the relationship between the bearing to prey and the proportion of the pursuit completed (**Fig. 5.11d**).



<u>Figure 5.11:</u> Variation in the angular difference between the predator's heading and the predator-prey line-of-sight, throughout the pursuit phase. (a) Definition of the angular difference between the predator's heading and the predator-prey line-of-sight. If the predator is heading towards a point ahead of the prey's current position, this value is positive (shown by the blue angle); when the predator is heading towards a point behind the prey's current position, the angle is negative (shown by the red angle). (b) Distribution of the angular difference between the predator's heading and the line-of-sight throughout the pursuit phase, in the predictable (blue) and unpredictable (pink) treatments. (c) Surface showing the interactive effects of the predator's maximum approach speed and the proportion of the pursuit completed on the predators' bearing to prey, derived from the generalised additive mixed-effects model receiving most support from the data (**Table 5.7**). (d) Change in the angular difference between the predator's heading and the line-of-sight over the course of the pursuit phase. Curves indicate the predicted values in predictable (blue) and unpredictable treatment (pink) trials, obtained from the second most likely generalised additive mixed-effects model (**Table 5.7**). Shaded regions represent the 95% confidence intervals surrounding each estimate.

Table 5.7: Results of GAMMs (generalised additive mixed models) predicting the difference between the predator heading angle and the predator-prey line-of-sight angle throughout the pursuit phase, based on data from 116 trials in which prey escaped an acute angle. Non-linear smooth terms are denoted by s(), and the total estimated degrees of freedom reflects both the number of parameters included in the model and the complexity of the penalised smooth terms.

Explanatory variables	**Total estimated degrees of freedom**	**AIC**	**ΔAIC**
s(Proportion of pursuit completed x Maximum predator approach speed) + s(Prey escape angle)	119.3	20908.3	0.00
s(Proportion of pursuit completed x Treatment) + s(Prey escape angle)	119.0	20911.6	3.17
s(Proportion of pursuit completed)	113.4	20916.5	8.21
s(Proportion of pursuit completed) + s(Prey escape angle) + Treatment	112.9	20917.1	8.78
s(Proportion of pursuit completed) + s(Prey escape angle)	112.9	20917.2	8.93
s(Proportion of pursuit completed) + s(Prey escape angle) + s(Maximum predator approach speed)	113.0	20918.5	10.21
Proportion of pursuit completed (linear effect)	106.9	21193.9	285.58
Null model (no explanatory variables)	105.4	21609.3	700.95

5.4.5 Distance to prey throughout the pursuit phase

In predator-prey interactions, the distance between the predator and the prey during an attack or throughout a pursuit might reflect the probability that the prey will ultimately evade capture. Therefore, I also investigated whether a slower approach impacted a predator's ability to stay within close proximity of its target over the course of the pursuit by focusing on whether predators lost ground during the pursuit (leading to a relative increase in the maximum predator-prey distance). The maximum predator-prey distance reached during the pursuit phase varied between trials, and in some cases the maximum predator-prey distance exceeded the initial predator-prey distance at the trigger point. However, there was no association between the maximum predator-prey distance and treatment, the treatment x trial number interaction or the maximum predator approach speed, as shown by the poor performance (or lack of improvement in model fit) of models including these variables relative to the null model (**Table 5.8**). Instead, the only model to represent a substantial improvement in fit over the null model was a model which included prey escape angle as an explanatory variable (**Table 5.8**), providing evidence for a positive relationship between prey escape angle and the maximum predator-prey distance during the pursuit (greater maximum distances occurred in trials in which the prey escaped at angles closer to 90°). For predators which approached prey more rapidly, the maximum predator-prey distance also occurred at an earlier point in the pursuit, but the timing of the maximum predator-prey distance was otherwise unaffected by treatment, trial number or the interaction between the two (**Table 5.9**), consistent with predators that approached quickly then rapidly closing in on the prey (**Fig. 5.7**). Further model comparisons (**Table 5.10**) also indicated that prey's escape angle was the strongest predictor of the rate of change of the predator-prey distance over the first half of the pursuit (as a proportion of the total pursuit duration), with a positive relationship between prey escape angle and this response variable. The rate of change of the predator-prey distance over the first half of the pursuit was also more negative for predators which approached at a higher maximum speed (**Table 5.10**), also consistent with the distance between the predator and its target declining more rapidly in these trials.

Table 5.8: Results of LMMs explaining variance in the maximum predator-prey distance during the pursuit, scaled as a proportion of the reaction distance (the distance between the predator and the prey, at the point when the escape response was triggered). Models were fitted to data from trials in which prey escaped at an acute angle (< 90°), consisting of 116 observations of 19 individual fish.

Explanatory variables	**Degrees of freedom**	**AICc**	**ΔAICc**
Prey escape angle	4	52.8	0.00
Treatment	4	54.9	2.02
Maximum predator approach speed	4	54.8	2.08
Null model (no explanatory variables)	5	55.3	2.55
Treatment x Trial number	6	59.9	4.00
Treatment + Trial number	5	56.9	4.15
Trial number	4	57.3	4.55

Table 5.9: Results of negative binomial GLMMs explaining the variation in the timing of the maximum predator-prey distance, over the course of the pursuit, based on 116 observations of 19 individual fish in trials where prey escaped at an acute angle (< 90°). All models include reaction distance as an explanatory variable to control for this effect.

Explanatory variables	**Degrees of freedom**	**AICc**	**ΔAICc**
Maximum predator approach speed + Reaction distance	5	186.2	0.00
Prey escape angle + Reaction distance	5	189.2	3.00
Trial number + Reaction distance	5	189.5	3.35
Reaction distance	4	189.7	3.51
Null model (explanatory variables)	3	189.9	3.72
Treatment + Trial number + Reaction distance	6	191.7	5.53
Treatment + Reaction distance	5	191.8	5.57
Treatment x Trial number + Reaction distance	7	192.8	6.63

Table 5.10: Results of LMMs explaining the variation in the rate of change in predator-prey distance during the first half of the pursuit. The first half of the pursuit was defined as period from when the prey started moving, until the time-point half-way between this start point and the moment the predator captured the prey. The analysis was based on 116 observations of 19 individual fish in trials where prey escaped at an acute angle (< 90°). All models include reaction distance as an explanatory variable to control for this effect.

Explanatory variables	**Degrees of freedom**	**AICc**	**ΔAICc**
Prey escape angle + Reaction distance	5	837.9	0.00
Predator maximum approach speed + Reaction distance	5	848.6	10.71
Null model (no explanatory variables)	3	852.8	14.95
Reaction distance	4	854.9	17.01
Trial number + Reaction distance	5	856.0	18.14
Treatment + Reaction distance	5	857.0	19.20
Treatment x Trial number + Reaction distance	7	857.9	20.36
Treatment + Trial number + Reaction distance	6	858.2	20.54

5.4.6 Speed and acceleration of the predator during the pursuit phase

For predators which rapidly approach prey programmed to escape at an acute angle, a reduction in speed or a momentary pause might enable the fish to adjust its heading in order to turn and pursue the escaping prey. A burst of acceleration might also be needed to compensate for a delay resulting from poor initial turning performance, leading to greater overall energy expenditure during the pursuit phase. To explore this further, model comparisons were used to identify the factors explaining variation in speed and acceleration during the pursuit phase. When considering the maximum speed reached by the predator during the pursuit phase, the model receiving most support from the data included maximum predator approach speed, reaction distance and prey escape angle as explanatory variables (**Table 5.11**). The difference in AICc values between this model and a model including only maximum predator approach speed and reaction distance was greater than 2 units, indicating that the prey's escape angle had a positive influence on the maximum speed reached during the pursuit. Moreover, consistent with initial expectations, predators which approached prey more rapidly also reached higher maximum speeds during the subsequent pursuit. This was demonstrated by the relative improvement in fit of a model featuring maximum predator approach speed and reaction distance, compared to the model which only included reaction distance as an explanatory variable (ΔAICc = 6.32, **Table 5.11**). As the average speed of the predator tended to peak at an early stage of the pursuit (**Fig. 5.12**), the positive relationship between the maximum approach and maximum pursuit speeds is likely to have arisen because predators which approached the prey rapidly also maintained high speeds in the initial portion of the pursuit phase. None of the other models tested represented an improvement in fit over the model including maximum predator approach speed and reaction distance (**Table 5.11**), suggesting that there was no additional effect of prey predictability on the maximum pursuit speed of the predator, or any effect of interactions between treatment and trial number or maximum predator approach speed or treatment.

If approach speed has an influence on the ability of the predator to turn sharply, pauses might be expected during the first half of the pursuit, just after the prey has started to escape. However, there was no association between the maximum approach speed of the predator and the minimum speed reached during the first half of the pursuit: the AICc value for the model which included maximum predator approach speed and reaction distance was similar to the null model containing no explanatory variables, suggesting that these models were approximately equivalent (**Table 5.12**). There was also no relationship between the maximum approach speed and the coefficient of variation in speed over the course of the pursuit, indicating that approach speeds were not associated with overall variability in speed during the pursuit (**Table 5.13**). Neither treatment, the treatment x trial number interaction or the treatment x maximum predator approach speed interaction had any substantial effect on the minimum speed of the predator or the coefficient of variation in speed during the pursuit of prey (**Tables 5.12-5.13**).

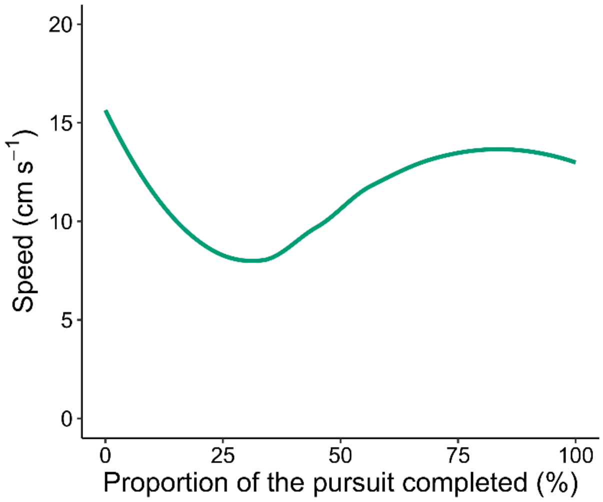


Figure 5.12: Speed of the predator throughout the pursuit phase. The curve shows a LOESS (locally weighted regression) fit to data from trials in which prey escaped at an acute angle (< 90°).

Table 5.11: Results of LMMs explaining the variation in the maximum speed of the predator over the course of the pursuit, based on 116 observations of 19 individual fish in trials where prey escaped at an acute angle (< 90°). All models include reaction distance as an explanatory variable to control for this effect.

Explanatory variables	**Degrees of freedom**	**AICc**	**ΔAICc**
Maximum predator approach speed + Reaction distance + Prey escape angle	6	659.7	0.00
Maximum predator approach speed + Reaction distance	5	666.3	6.67
Maximum predator approach speed + Reaction distance + Treatment	6	668.2	8.48
Maximum predator approach speed + Reaction distance + Trial number	6	668.5	8.76
Maximum predator approach speed + Reaction distance + Treatment + Trial number	7	670.5	10.73
Maximum predator approach speed x Treatment + Reaction distance	7	670.5	10.74
Reaction distance	4	672.7	12.99
Maximum predator approach speed + Reaction distance + Treatment x Trial number	8	672.7	13.00
Null model (no explanatory variables)	3	672.9	13.18

Table 5.12: Results of LMMs explaining the variation in the minimum speed of the predator, during the first half of the pursuit phase, based on 116 observations of 19 individual fish in trials where prey escaped at an acute angle (< 90°).

Explanatory variables	**Degrees of freedom**	**AICc**	**ΔAICc**
Maximum predator approach speed + Reaction distance + Trial number	6	764.1	0.00
Maximum predator approach speed + Reaction distance	5	764.2	0.06
Null model (no explanatory variables)	3	764.6	0.49
Maximum predator approach speed + Reaction distance + Prey escape angle	6	765.1	1.04
Maximum predator approach speed + Reaction distance + Treatment	6	765.7	1.55
Maximum predator approach speed + Reaction distance + Treatment + Trial number	7	765.8	1.71
Reaction distance	4	766.0	1.89
Maximum predator approach speed x Treatment + Reaction distance	7	767.6	3.46
Maximum predator approach speed + Reaction distance + Treatment x Trial number	8	768.1	4.01

Table 5.13: Results of Gamma GLMMs predicting the degree of variation in speed for each trial (i.e. coefficient of variation for speed) over the course of the pursuit, based on 116 observations of 19 individual fish in trials where prey escaped at an acute angle (< 90°).

Explanatory variables	**Degrees of freedom**	**AICc**	**ΔAICc**
Reaction distance	4	1012.9	0.00
Null model (no explanatory variables)	3	1014.3	1.41
Maximum predator approach speed + Reaction distance + Treatment	6	1014.9	1.94
Maximum predator approach speed + Reaction distance	5	1016.4	1.97
Maximum predator approach speed + Reaction distance + Trial number	6	1016.4	3.50
Maximum predator approach speed x Treatment + Reaction distance	7	1016.6	3.67
Maximum predator approach speed + Reaction distance + Treatment + Trial number	7	1016.8	3.82
Maximum predator approach speed + Reaction distance + Prey escape angle	6	1016.8	3.91
Maximum predator approach speed + Reaction distance + Treatment x Trial number	8	1019.0	6.04

After controlling for the predator's maximum approach speed and the predator-prey reaction distance, further model comparisons revealed that the prey's escape angle had the strongest effect on maximum acceleration during the pursuit phase (**Table 5.14**), with predators accelerating more at higher escape angles, closer to 90°. There was also evidence for an effect of treatment on the maximum acceleration of the predator, as the model featuring maximum predator approach speed, reaction distance and treatment as explanatory variables received more support from the data than the baseline model including only maximum predator approach speed and reaction distance (ΔAICc = 2.07, **Table 5.14**). In predictable treatment trials, fish did not accelerate as much (reached lower maximum acclerations) when pursuing prey compared to the unpredictable treatment (**Fig. 5.13a**). There was however no evidence for an association between the predator's maximum approach speed and maximum acceleration during the pursuit (**Fig. 5.13b**), as the model including maximum predator approach speed and reaction distance received less support from the data than a model including only reaction distance (ΔAICc = 1.59, **Table 5.14)**, demonstrating that the inclusion of maximum approach speed resulted in a poorer fit. There was also no evidence to suggest that the maximum acceleration of fish was influenced by a treatment x trial number interaction, or an interaction between maximum predator approach speed and treatment (**Table 5.14**). The latter might be expected if predators had to compensate for the effects of a rapid approach by accelerating in the pursuit phase, but only when prey had escaped in an unexpected direction (in the unpredictable treatment).

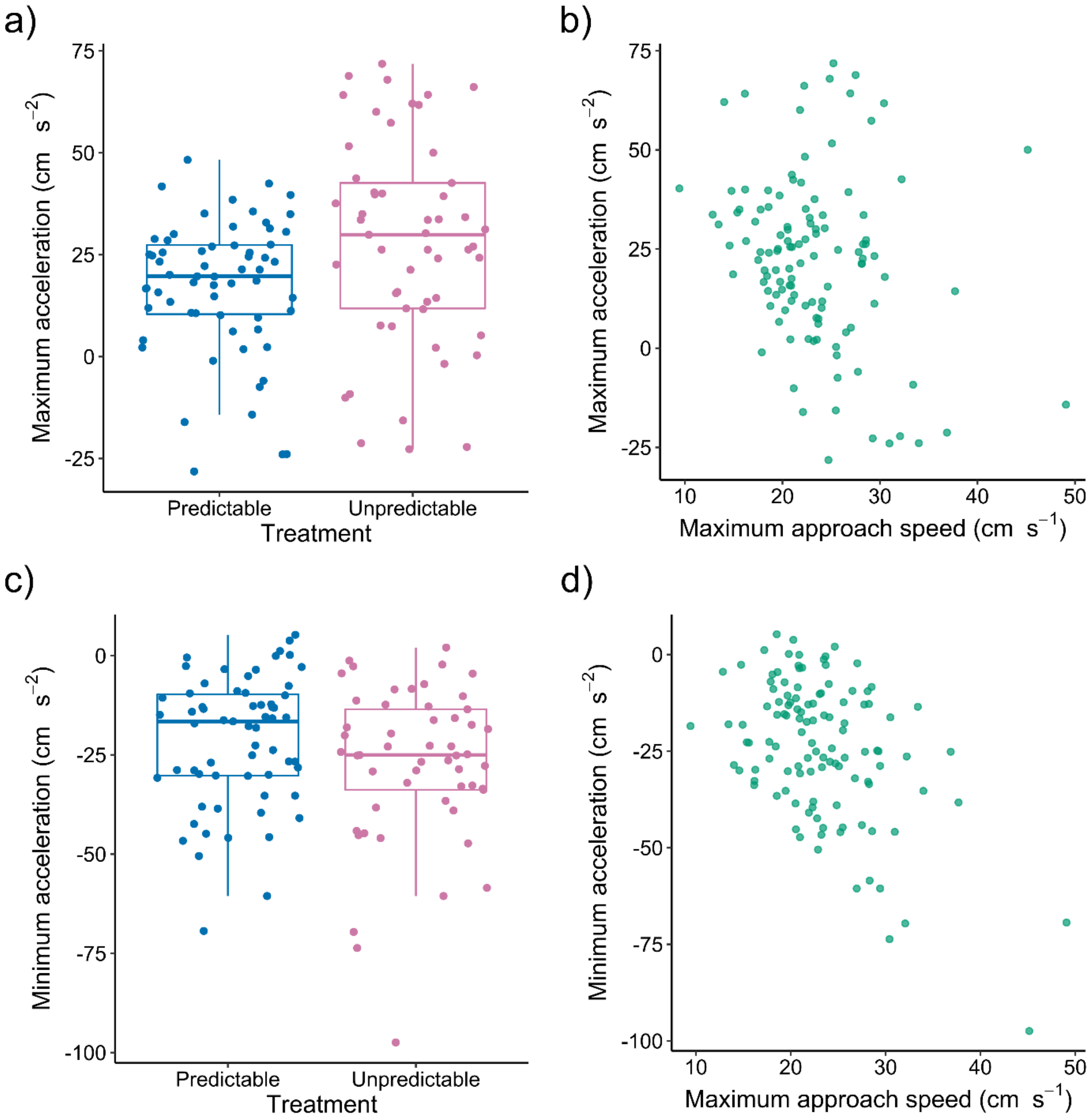


Figure 5.13: Relationship between treatment (predictable vs. unpredictable) (a, c) or maximum predator approach speed (b, d), and maximum acceleration of the predator during the pursuit phase (a-b) or minimum acceleration of the predator during the first half of the pursuit (c-d).

Table 5.14: Results of LMMs explaining variation in the maximum acceleration of the predator throughout the pursuit, based on 116 observations of 19 individual fish in trials where prey escaped at an acute angle (< 90°).

Explanatory variables	Degrees of freedom	AICc	ΔAICc
Maximum predator approach speed + Reaction distance + Prey escape angle	6	1020.4	0.00
Maximum predator approach speed + Reaction distance + Treatment	6	1027.0	6.56
Reaction distance	4	1027.4	7.04
Maximum predator approach speed + Reaction distance + Treatment x Trial number	8	1027.8	7.42
Maximum predator approach speed x Treatment + Reaction distance	7	1028.3	7.92
Maximum predator approach speed + Reaction distance	5	1029.9	8.63
Maximum predator approach speed + Reaction distance + Treatment + Trial number	7	1029.2	8.83
Maximum predator approach speed + Reaction distance + Trial number	6	1031.2	10.85
Null model (no explanatory variables)	3	1031.7	11.31

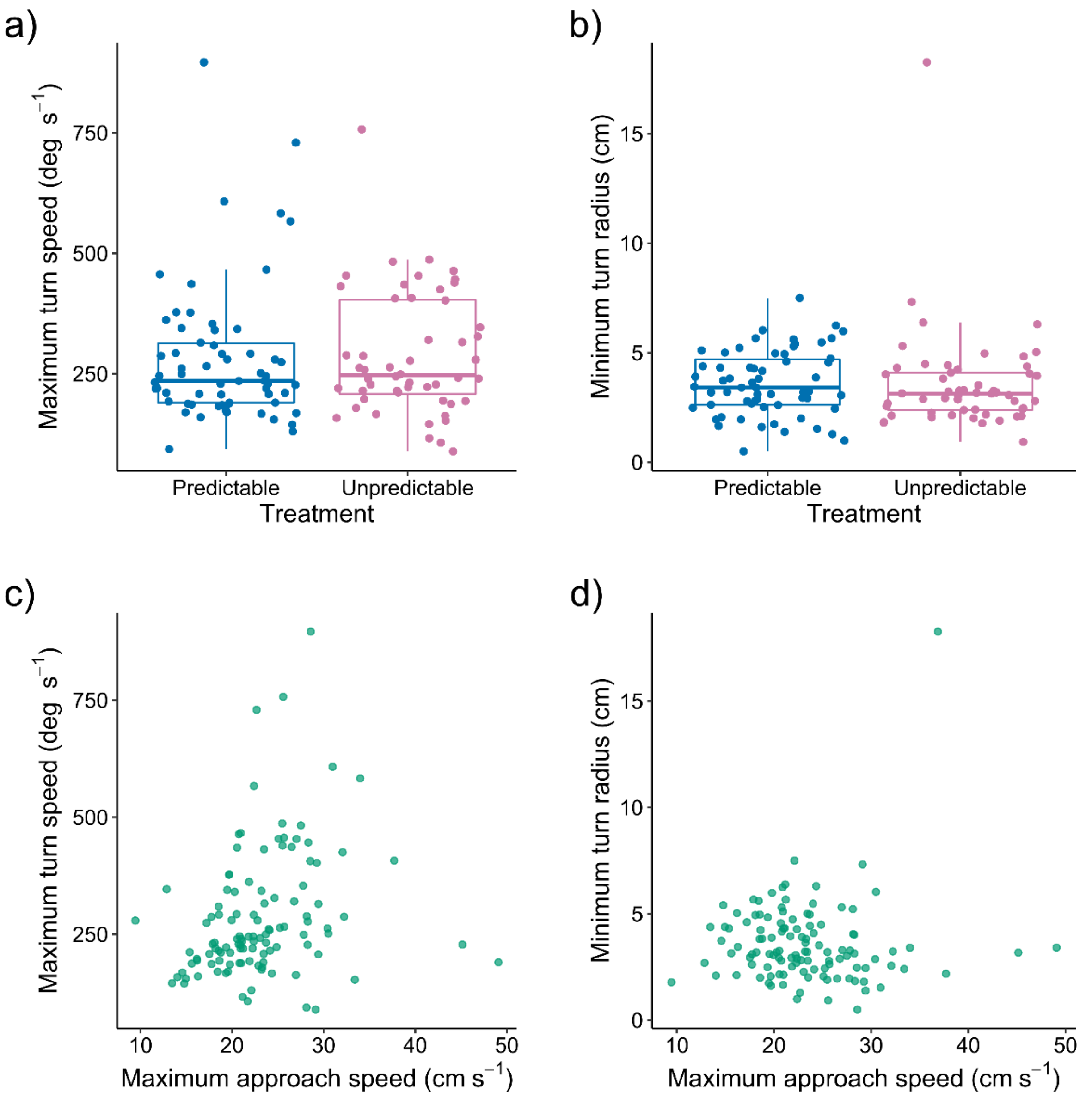
The experimental treatment (predictable vs. unpredictable) was not a statistically important predictor of the predator's minimum acceleration during the first half of the pursuit (**Fig. 5.13c**), as indicated by the fact that the AICc value for the model including treatment, maximum predator approach speed and reaction distance received less support from the data than a baseline model which included only maximum predator approach speed and reaction distance (ΔAICc = 2.22, **Table 5.15**). Compared to this baseline model, only the model featuring trial number, maximum predator approach speed and reaction distance represented a substantial improvement (ΔAICc = 3.69): inspection of model coefficients demonstrated that the minimum acceleration was positively correlated with trial number. The relatively large difference in AICc scores (ΔAICc = 28.45) between the model including maximum predator approach speed and reaction distance and the model which only included reaction distance also indicated that the predator’s maximum approach speed was strongly negatively correlated with its minimum acceleration during the pursuit phase (**Fig. 5.13d**).

Table 5.15: Results of LMMs explaining variation in the minimum acceleration of the predator, over the first half of the pursuit, based on 116 observations of 19 individual fish in trials where prey escaped at an acute angle (< 90°). This first half of the pursuit was defined as period from when the prey started moving, until the time-point half-way between this start point and the moment the predator captured the prey.

Explanatory variables	**Degrees of freedom**	**AICc**	**ΔAICc**
Maximum predator approach speed + Reaction distance + Trial number	6	906.9	0.00
Maximum predator approach speed + Reaction distance + Treatment x Trial number	8	963.0	2.14
Maximum predator approach speed + Reaction distance + Prey escape angle	6	963.1	2.18
Maximum predator approach speed + Reaction distance + Treatment + Trial number	7	963.1	2.25
Maximum predator approach speed + Reaction distance	5	964.9	3.69
Maximum predator approach speed + Reaction distance + Treatment	6	966.8	5.91
Maximum predator approach speed x Treatment + Reaction distance	7	968.9	8.06
Reaction distance	4	993.0	32.14
Null model (no explanatory variables)	3	995.0	34.09

5.4.7 Turning ability of the predator during the pursuit phase

Turning ability can be assessed by examining both the rate of change in its direction (maximum turning rate) and how sharply an animal turns (indicated by the minimum radius of curvature, Combes *et al*. 2012). Comparisons between models featuring these variables as a response indicated that the maximum turn speed and minimum turn radius were unaffected by treatment (**Fig. 5.14a-b**, **Tables 5.16-5.17**). Furthermore, there was no evidence for a relationship between either of these variables and the maximum speed of the predator during the approach (**Fig. 5.14c-d**, **Tables 5.16-5.17**).



<u>Figure 5.14:</u> Relationship between treatment (predictable vs. unpredictable) (a-b) or maximum predator approach speed (c-d), and the maximum turn speed (a, c) or the minimum turn radius (b, d) of the predator during the pursuit phase.

Table 5.16: Results of Gamma GLMMs explaining variation in the maximum turning speed of the predator during the pursuit phase, based on 116 observations of 19 individual fish in trials where prey escaped at an acute angle (< 90°).

Explanatory variables	**Degrees of freedom**	**AICc**	**ΔAICc**
Prey escape angle	4	1679.5	0.00
Treatment + Prey escape angle	5	1681.0	1.51
Trial number	4	1682.0	2.51
Treatment x Prey escape angle	6	1682.2	2.68
Null model (no explanatory variables)	3	1683.2	3.68
Treatment + Trial number	5	1684.0	4.53
Treatment	4	1685.1	5.59
Maximum predator approach speed	4	1685.3	5.81
Treatment x Trial number	6	1685.7	6.18
Treatment + Maximum predator approach speed	5	1687.3	7.76
Treatment x Maximum predator approach speed	6	1687.3	7.80

Table 5.17: Results of LMMs explaining variation in the minimum turn radius of the predator during the pursuit phase, based on 116 observations of 19 individual fish in trials where prey escaped at an acute angle (< 90°).

Explanatory variables	**Degrees of freedom**	**AICc**	**ΔAICc**
Prey escape angle	4	1679.5	0.00
Treatment + Prey escape angle	5	1681.0	1.51
Trial number	4	1682.0	2.51
Treatment x Prey escape angle	6	1682.2	2.68
Null model (no explanatory variables)	3	1683.2	3.68
Treatment + Trial number	5	1684.0	4.53
Treatment	4	1685.1	5.59
Maximum predator approach speed	4	1685.3	5.81
Treatment x Trial number	6	1685.7	6.18
Treatment + Maximum predator approach speed	5	1687.3	7.76
Treatment x Maximum predator approach speed	6	1687.3	7.80

5.5 Discussion

5.5.1 Effects of the predictability of the prey's escape angle on predator behaviour

The effects of prey unpredictability on predator behaviour have previously been considered by testing the impact of erratic prey movements on the capacity of predators to track or intercept a continuously moving target (Jones, Jackson and Ruxton, 2011; Combes *et al*., 2012; Richardson *et al*., 2018). By contrast, the primary aim of this study was to test whether unpredictability in the initial escape angle of prey prevents predators from learning to adjust their approach and pursuit behaviour over the course of multiple interactions (Domenici, Blagburn and Bacon, 2011b). My analysis focused initially on the maximum speed of the predator during the approach phase, as during this period the only information available to the predator about the prey's escape direction was that gained from interactions in previous trials. If unpredictability prevents predators from anticipating the prey's escape trajectory, increasing experience with unpredictable prey is likely to have a limited effect on the predator's approach behaviour. Conversely, over the course of multiple trials with predictable prey, predators might be expected to adjust their approach or to optimise aspects of their pursuit behaviour. Contrary to these expectations, predators approached prey more rapidly as they gained more experience regardless of the experimental treatment (i.e. trial number had a positive influence on the predator's approach speed, but there was no evidence for an interaction between treatment and trial number). However, approach speeds were also influenced by an interaction between treatment and the prey's escape angle. In the predictable treatment, predators approached prey programmed to escape directly away from them more rapidly than prey programmed to escape at an acute angle, but for unpredictable prey there was no relationship between the predator's approach speed and the prey's escape angle. This positive relationship between maximum approach speed and prey escape angle in the predictable treatment was not explained by differences between individual predators in traits which could influence approach speeds, such as body size or a proxy for the predator's motivation. As the two experimental treatments only differed in the predictability of the prey’s initial escape angle, this suggests that predators adjusted their approach speed when relatively certain about the direction prey would escape in. While these results are consistent with an effect of prey predictability on the predator’s approach behaviour, without direct evidence that the effect of trial number on predator behaviour differed between the two treatments, it is difficult to conclude with a high degree of confidence that unpredictability obstructs the ability of predators to learn about the prey’s escape direction. Considered together, these findings therefore provide only limited and tentative support for the original hypothesis that unpredictable prey escape angles function to prevent learning by predators.

Despite the finding that prey predictability influences the relationship between the escape angle of prey and the maximum approach speed of the predator, the positive effect of increasing experience on the predator’s approach speed did not differ between the two treatments. If it was advantageous for predators to approach prey programmed to flee directly away from them at higher speeds, predators would be expected to increase their approach speed as they become more experienced with prey which repeatedly escape at this angle. However, there was no evidence that maximum predator approach speeds were influenced by a three-way interaction between trial number, treatment and prey escape angle. There were also considerable differences between individuals in the effect of trial number, with some fish showing an increase in approach speed with trial number and others showing a decrease. Any effect of prey predictability on learning might therefore have been masked by differences in the speed of learning between individual fish (Cauchoix *et al.*, 2018). Differences between the two treatments in the influence of experience on predator behaviour could also have been partially obscured by the fact that short runs of consecutive trials with similar prey escape angles were possible in the unpredictable treatment, even though angles were drawn randomly in each trial.

5.5.2 Relationships between predator approach speed, prey escape angle and the behaviour of the predator in the pursuit phase

Predators which approached prey more rapidly took less time to capture prey, regardless of the prey's escape angle. In the predictable treatment, this can explain why predators approached at a higher speed when attacking prey programmed to escape directly away from them, as a rapid approach enabled predators to swiftly catch up with their target. Yet, given that the benefit of a rapid approach applies equally across all prey escape angles, this result raises the question of why predators did not approach more rapidly when exposed to prey programmed to escape consistently at an acute angle, even though fish are likely to have had the capacity to approach at higher speeds. There was also no evidence of an interactive effect of treatment and the prey's escape angle on the time taken to capture prey, even though the predator's maximum approach speed was influenced by the interaction between these two variables. In trials in which prey escaped at an acute angle, one potential explanation for these results might be that blue acaras can compensate for a slower approach by improving their performance in the pursuit phase, but only when prey are predictable. This possibility was addressed by examining the consequences of variation in approach speed on the behaviour of the predator during the pursuit, and exploring various ways in which increased approach speeds might be costly, or reduced speeds might be advantageous.

Overall, the results of this analysis provide little evidence to support the idea that predators adaptively reduced their speed. Firstly, when chasing down prey, predators appeared to follow a pure pursuit strategy, and there was no indication that a reduction in approach speed allowed predators to pursue prey more efficiently by deviating from pure pursuit and attempting to intercept prey. Moreover, over the course of pursuit, the directional heading of predators which approached prey at higher speeds also remained more aligned towards the prey throughout the pursuit, suggesting that predators which approached more rapidly tracked the movements of prey more effectively than those approaching more slowly. Secondly, predators' maximum approach speeds were not correlated with measures of turning performance when pursuing prey which escaped at an acute angle. Although the speed-manoeverability trade-off is well established in fish, it is typically mediated by differences in body size between species (Domenici, 2001). The results of this experiment suggest that over the range of approach speeds exhibited by predators in these trials, high speed approaches did not come at the cost of reduced turning ability. Thirdly, there was only limited evidence that predators approaching at higher speeds had to compensate for reduced performance in the pursuit phase. If approaching prey more rapidly puts predators at a disadvantage when faced with prey which escape at an acute angle, compensatory bursts of acceleration by the predator are likely to be reflected in the speed or acceleration profile of the predator during the pursuit. Predators did accelerate more sharply when pursuing unpredictable prey compared to predictable prey, but there was no discernible effect of maximum approach speed on variability in speed during the pursuit phase, or on the maximum acceleration of the predator. There was also no evidence for an interaction between maximum approach speed and treatment, as might be expected if compensatory bursts of acceleration are necessary to catch up with prey after approaching too quickly, but only when prey flee in an unexpected direction. Additionally, the negative relationship observed between the predator’s maximum approach speed and minimum acceleration during the pursuit is most likely due to the fact that predators which approached more rapidly had to reduce their distance to the prey more quickly, and were thus forced to decelerate more than predators approaching more slowly. By failing to pinpoint a clear benefit to slowing down or a cost of speeding up, these results make it difficult to identify the cause of the apparent reduction in approach speed, which was observed when blue acaras faced prey programmed to predictably escape at an acute angle. As a consequence, the behaviour of predators in the predictable treatment is perhaps best explained by a model in which predators actively increased their approach speed when faced with prey programmed to escape directly away from them, but did not deviate from a baseline approach speed over repeated encounters with prey programmed to escape at an acute angle. Intermediate approach speeds shown by predators in the unpredictable treatment may also represent a form of insurance aimed at keeping options open when faced with unalterable uncertainty about the prey's likely escape direction (Dall, 2010).

In their natural environment, blue acara cichlids are opportunistic predators which actively pursue prey such as guppies (Botham *et al*., 2006). The results of this study are therefore more relevant to predator-prey interactions involving pursuit predators which reactively adjust their trajectory in response to fleeing prey, rather than to predator-prey systems involving specialist ambush or stalk-and-strike predators which attack prey at close range using a powerful fast-start reflex, and have little opportunity to adjust their trajectory in the period immediately after an initial strike (Webb, 1984). Geometry-based models of predator-prey interactions suggest that an effective prey escape strategy against pursuit predators may be to wait until the predator has approached within an intermediate range before executing a sharp turn towards its flank, with the aim of entering a region of space in which it is difficult for the predator to capture the prey without a sharp and immediate body rotation (Howland, 1974; Corcoran and Conner, 2016). This strategy is reminiscent of the prey escape response in trials in which prey escaped an acute angle. The relatively slow approach speeds shown by acaras in the predictable treatment, when repeatedly presented with prey escaping at an angle of 90 degrees of less, could be therefore interpreted as an attempt to counter this escape tactic by giving the predator more time to react. Crucially however, if this were the case, predators approaching prey programmed to escape at an acute angle at high speeds would be expected to incur a cost, as a consequence of failing to adjust their approach speed. Given the evidence that strike accuracy typically declines with attack speed in fish (Webb and Skadsen, 1980; Higham, Day and Wainwright, 2006), one possible reason why there was no apparent disadvantage to a rapid approach in this experiment is that the experiment was not designed to measure fine-grained aspects of the final attack sequence, including how the fish handled the prey upon capture. Approaching the prey at a sufficiently high speed may also have enabled predators to minimise distance to the prey in the initial moments of the pursuit, rendering any escape strategies ineffective regardless of the prey escape angle (Corcoran and Conner, 2016). Alternatively, since dramatic lateral movements by escaping prey can potentially compromise the ability of visual predators to track their target (Kane, Fulton and Rosenthal, 2015), the apparent reduction in approach speed shown by acaras could also reflect the need to reduce the rate at which the predator advances towards its target, which may help to maintain the escaping prey at the centre of the predator's visual field.

5.5.3 Implications for unpredictability as a prey escape tactic

Over a series of encounters, a lack of consistency in the initial escape angle of prey might appear to be unpredictable from the predator's perspective, but the variability in escape direction which has been observed in multiple studies could also have arisen for a range of other reasons (Domenici, Blagburn and Bacon, 2011a). While the initial escape angles of many prey taxa are often highly variable within a limited angular range, with some species showing preferences for several widely separated escape angles (Arnott, Neill and Ansell, 1999; Domenici, Blagburn and Bacon, 2011a; Bateman and Fleming, 2014), in other predator-prey systems even minor deviations from the optimal escape angle can have a significant effect on survival (Fuiman, 1993; Walker *et al*., 2005). Although for a given predator-prey speed ratio, models of predator-prey interactions predict that prey will adopt a single optimal escape angle which maximises the distance to the approaching threat (Weihs and Webb, 1984; Domenici, 2002), recent extensions of these classic models suggest that these expectations will not apply across all predator-prey systems. For example, deviations from theoretically optimal escape angles can have important consequences for survival when the predator's approach speed is similar to the prey's escape speed, but are expected to have little impact when predators are much slower than their prey (Soto, Stewart and McHenry, 2015). Under these conditions, variability in prey escape angles could simply reflect the equal effectiveness of escape responses across a range of angles, rather than an adaptation to prevent predators from learning to anticipate the movement of their target (Nair, Nguyen and McHenry, 2017). Relaxing the potentially unrealistic assumption that prey are capable of instantaneously escaping in any direction, irrespective of their orientation relative to the predator, also has the potential to account for the existence of multiple preferred escape angles, suggesting that unpredictability could arise as a by-product of constraints on the ability of prey to select the optimal angle (Kawabata *et al*., 2020).

Instead of representing a generally effective escape strategy for prey, the advantages of incorporating variability into the initial escape response are also likely to vary between specific predator-prey systems. A degree of unpredictability may be particularly important in systems in which predators attack at high speed, triggering an equally rapid prey escape response at a fractionally later time-point. In this type of scenario, unpredictability might confer a survival advantage if the predator cannot modify the trajectory of its strike in the brief moments following an attack, as is often the case with predators which ambush or stalk their prey (Walker *et al*., 2005; Heathcote *et al*., 2020). The effectiveness of unpredictability as an escape tactic could also depend on the extent to which the predator's typical attack strategy performs equally well across a range of prey escape directions, or whether these tactics require modification in order to capture prey escaping at a specific angle. Consistent with this idea, one recent study has demonstrated that the prey escape angle which maximises survival depends on the precise aiming point of the predator along the length of the prey's body (Heathcote *et al*., 2020), highlighting the potential for subtle variation in the strike trajectory of the predator to influence the outcome of an attack. Predicting the scope for unpredictability to act as a viable escape tactic is therefore likely to rely on detailed knowledge of the biomechanical constraints operating on predators and prey during a typical interaction. More research is also required to understand the ecological context in which behavioural unpredictability might enhance the effectiveness of anti-predator defences. For example, little is known about how the availability of alternative prey types might affect the response of predators to prey escape strategies over time. For a given prey species, more infrequent encounters with a predator might be expected when predators regularly target a wide range of other prey types. This could potentially limit the benefits of being unpredictable, particularly if species-level differences in escape strategies are sufficient to generate unpredictability from the predator’s point of view (Hügel and Goerlitz, 2019). On the other hand, in ecological contexts where alternative prey are scarce, predators may show greater persistence in their attempts to capture the same prey type, potentially selecting for greater unpredictability.

5.5.4 Limitations and opportunities of the robotic prey system

Although the robot-controlled prey in this study followed a widely observed escape strategy, in which prey are initially stationary but flee following a predator attack (Cooper and Blumstein, 2015), several aspects of robotic prey behaviour were simplified, compared to real prey. While robotic prey in this study were programmed to respond to an approaching blue acara cichlid, representing a key difference between this experiment and previous studies which have examined the effects of prey unpredictability using unresponsive virtual prey (Jones, Jackson and Ruxton, 2011; Richardson *et al.*, 2018), the prey’s escape tactics were nonetheless pre-determined at the start of each trial. Whereas in this experiment, the prey escape response was triggered by the approach of the predator within a pre-specified threshold distance, the reaction distances of real prey are sometimes positively correlated with the predator’s approach speed (Dill, 1974; Webb, 1982; Domenici, 2002; Cooper, 2006) or modulated by other factors which influence the perceived risk of predation (Dill, 1990). While this lack of responsiveness to fine-scale differences in the behaviour of the attacking predator can be viewed as a limitation, this aspect of the experimental design was criticial in enabling the effect of escape angle predictability to be isolated from other components of the escape response. It would be possible to address this in future experiments by adjusting the program used to control the movements of the robotic prey, so that prey escape responses are explicitly connected to fine-grained aspects of predator behaviour which indicate risk, including the predator’s approach speed. If prey were programmed to react to a speedily approaching predator by fleeing at greater distances, and future experiments were to include a refuge zone which is inaccessible to the predator, this may compel predators to approach prey more slowly, and delay a high speed attack until the last possible moment.

The robot prey system developed here can also be adapted and extended to test the effectiveness of a range of different prey anti-predator tactics, and the capacity of predators to counteract these strategies by learning. In future experiments, artificial prey could be programmed to move in a more realistic way, by incorporating greater complexity in the prey's escape path. Simulations of pursuit behaviour based on data from avian predators have suggested that steering control or guidance laws which result in a trajectory closely approximating a pure pursuit are more effective against erratically moving targets, as the predator is less likely to be thrown off course when the prey executes a series of sharp turns at close range (Brighton and Taylor, 2019). Manipulating the tortuosity or turning angle of the prey's escape path would enable an experimental test of whether aquatic predators can optimise their pursuit strategy in response to prey escape behaviour over many repeated chases, and provide an insight into the degree of experience required to develop sophisticated targeting techniques. More broadly, an approach based on experimentally manipulating prey behaviour could help address the question of which predator pursuit strategies perform best against different prey escape tactics, which remains difficult to address without the use of responsive artificial prey (Hein *et al.*, 2020).

Chapter 6:

Synthesis and future directions for research on the consequences of predator personality and cognition for predator-prey interactions

Still image from a video recording showing a pike cichlid (*Crenicichla frenata*)
approaching the stimulus guppy shoal, Lopinot River, Trinidad.
Photograph: A. W. Szopa-Comley.

6.1 Abstract

The overall aim of this thesis was to explore the effects of predator personality and cognition on predator-prey interactions, with an emphasis on later stages of the predation sequence. Firstly, in Chapter 2, an experiment with three-spined sticklebacks revealed that inter-individual variation in the time taken for fish to attack cryptic or conspicuous prey was not explained by the time taken to leave a refuge, a measure of boldness. Contrary to expectations based on a trade-off between attention allocated towards searching for prey and vigilance, these results did not support the existence of an association between predator boldness and prey detection. Secondly, the results of a field experiment on pike cichlids, presented in Chapter 3, provided additional support for the conclusion that boldness does not always predict ecologically relevant aspects of predator behaviour. Consistent inter-individual variation in the response of pike cichlids to a stimulus prey shoal was found to be independent of the factors influencing encounter rates with the empty apparatus, including boldness, and is likely to constitute a predation-specific personality trait. Thirdly, when guppies were exposed to pike cichlids in artificial experimental pools, as outlined in Chapter 4, the boldness of individual predators (assessed separately in trials without prey) was not related to the intensity of the prey's anti-predator response, suggesting that boldness was not relevant to the prey's perception of risk. Finally, in Chapter 5, an experiment involving repeated interactions between blue acara cichlids and artificial robot-controlled prey was conducted to test the impact of predictable and unpredictable prey escape angles on predator behaviour. While there was no direct indication that the unpredictable prey escape strategy inhibited learning by predators, there was evidence to suggest that predators modulated the speed of their approach according to the prey's escape angle, but only when the prey's escape angle was predictable. Although the individual fish tested in Chapter 5 did not differ repeatably in their boldness, a fruitful area of future research would be to explore the impact of personality variation on the capacity of predators to adjust their behaviour in response to prey.

6.2 General conclusions on the effects of predator personality and cognition on predator-prey interactions, and their potential implications

6.2.1 Boldness is not always a reliable predictor of the risk posed by individual predators

A persistent criticism of many studies of animal personality is that widely studied personality traits fail to target the traits which are most ecologically relevant to the species in question (Réale *et al*., 2007; Carter *et al*., 2013; Dall and Griffith, 2014; Koski, 2014). A focus on ecologically relevant behavioural traits may be particularly important when the goal of the research is to examine or predict the consequences of personality variation for a specific ecological process (Koski, 2014). At first glance, the propensity of individual predators to accept a measure of risk in the pursuit of profitable prey might be expected to have pervasive effects on predator-prey interactions, as predators often face threats from their own predators as well as from dangerous prey (Mukherjee and Heithaus, 2013; Michalko and Pekar, 2017). Indeed, previous studies on the consequences of predator personality variation suggest that bolder predators move through their environment at a higher rate and spend more time actively searching for prey than shy predators, leading to higher rates of prey consumption by bold individuals (Ioannou, Payne and Krause, 2008; Griffen, Toscano and Gatto, 2012; Toscano and Griffen, 2014).

Despite the emphasis on boldness and activity levels in prior research on predator personality (see Chapter 1), three lines of evidence from this thesis suggest that the bold-shy behavioural axis is not a reliable predictor of the risk posed by an individual predator in all circumstances. Firstly, as detailed in Chapter 2, repeated presentations of conspicuous and cryptic prey to three-spined sticklebacks revealed that individual fish differed in the time taken to attack prey, an indirect measure of prey detection. Counter to predictions based on the expected role of attention in visual search (Dukas, 2002), differences between individuals in the time taken to attack were not explained by the boldness levels of individual fish. Secondly, as demonstrated in Chapter 3, individual pike cichlids differed consistently in their response to prey, with some individual predators spending more time in close proximity of prey than others. Crucially, these differences were not accounted for by the response of the same individual predators to the experimental apparatus lacking prey, which is likely to have been indicative of the factors influencing encounter rates, including individual boldness levels. Thirdly, when pike cichlids and guppies were exposed to one another in the experimental pools described in Chapter 4, the boldness of individual pike cichlids was not associated with variation in the strength of the prey anti-predator response, averaged over the course of a trial, suggesting that the level of risk perceived by prey was not sensitive to the boldness levels of the predator.

Although this thesis has addressed the topic of animal personality, focusing on the potential links between boldness and more ecologically relevant aspects of predator behaviour, individual fish did not always differ repeatably in the behavioural variables used as the boldness measure. For example, in Chapter 3, individual pike cichlids did not differ repeatably in their behaviour during control presentations, in which the experimental apparatus was presented without prey. As personality traits are typically defined as consistent inter-individual differences in behaviour (Réale *et al*., 2007), this raises the question of whether these tests adequately captured inter-individual variation in boldness. Firstly, when considering this possibility, it is important to note that the approach of assessing boldness using an empty experimental apparatus in the field, functioning as a novel object, has several advantages. The approach of testing animals *in situ* can avoid problems that occur with tests conducted under controlled conditions, which can inadvertently measure an individual’s responsiveness to the stress induced by an artificial environment, rather than the trait they intend to target (Niemelä and Dingemanse, 2014). Novel object presentations are also widely used in field studies to quantify the tendency of individuals to take risks, as novelty can be regarded as a potential hazard (Dammhahn and Almeling, 2012; Patrick, Pinaud and Weimerskirch, 2017; Harris *et al*., 2019). While not repeatable, the behaviour of individual fish during control presentations is therefore still likely to reflect their response to an unfamiliar object, particularly in the initial presentation, when the experimental apparatus had not been previously encountered by the fish within a pool. Importantly, the results presented in Chapter 3 show that consistent inter-individual differences in the response of pike cichlids to prey were not explained by the behaviour of the same individuals during control presentations, even when considering just the behaviour of fish in the initial control presentation (Section 3.4.5). This result therefore suggests that inter-individual variation in the response to prey was independent of the reaction to a potentially hazardous novel object.

Secondly, the lack of repeatability in the behaviour of individual fish during control presentations does not necessarily mean that these presentations failed to target boldness. Instead, it might suggest that boldness itself is not repeatable when measured under these conditions. Previous research has demonstrated that the strength of personality expression can sometimes depend on the specific context in which testing occurs (van Oers, Klunder and Drent, 2005; Carter *et al*., 2013). For a given behavioural trait, which differs repeatably between individuals in one particular context, the expression of consistent inter-individual differences can be amplified in other situations, leading to higher levels of repeatability (Dammhahn and Almeling, 2012). Alternatively, in another context, individuals may behave in a similar way, resulting in the erosion of repeatable differences (Kluen and Brommer, 2013; Fisher *et al*., 2015; McDonald *et al*., 2016). A lack of repeatable differences in boldness may arise because the environmental context is insufficiently risky for behavioural differences between individuals to become apparent, or because the level of background risk favours convergence on the same behavioural phenotype (Couchoux and Cresswell, 2012). By demonstrating that individual pike cichlids did not differ consistently in their behaviour when repeatedly tested over multiple control presentations, which are comparable to typical boldness tests, the results presented in Chapter 3 indicate that the individual fish within this population exhibit similar levels of boldness to each other under natural conditions. Crucially, boldness, as measured here, was insufficient to explain consistent differences in the response of individual pike cichlids to prey.

While further research is required to confirm the generality of these findings, the results presented in this thesis imply that the boldness of the predator may not be relevant to events occurring later in the predation sequence, taking place after an encounter has occurred. These findings mirror those obtained from research on the selective pressures generated by recreational fisheries. Numerous studies have sought to identify the behavioural traits which predispose individual fish to capture via fishing techniques such as angling, which relies on the use of baits or prey-mimicking lures (Diaz Pauli and Sih, 2017). Although it is often the case that bold fish are caught more frequently by anglers (Härkönen *et al*., 2014; Wilson *et al*., 2015; Diaz Pauli and Sih, 2017), boldness does not predict susceptibility to angling in predatory fish species which rely on ambush tactics to capture their prey (Louison *et al*., 2017). For these species, the link between boldness and encounter rates may have little bearing on the tendency to strike at bait or a lure, which can be viewed as being analogous to prey. Importantly, research in this field has also shown that consistent inter-individual differences in movement and space use are not always significant drivers of variation in susceptibility to capture via angling (Monk and Arlinghaus, 2017), implying that the behavioural factors influencing encounter rates are distinct from the determinants of the decision to attack.

The results presented in Chapters 2-4 also lead to the prediction that boldness will have a larger effect on prey survival in predator-prey systems in which the probability of capture is largely determined by, or proportional to, encounter rates. Conversely, boldness is likely to be less important in systems in which there is considerable variation in the probability of capture given an encounter, and encounter rates are therefore less influential. The latter situation might arise when predators and prey spend a large proportion of their daily time budget within close range of one another, or when predation risk is largely determined by topography or habitat characteristics rather than predator-prey encounter rates (Hebblewhite, Merrill and McDonald, 2005; Kauffmann *et al*., 2007; Wirsing, Heithaus and Dill, 2007; Cresswell and Quinn, 2013; Catano *et al*., 2016). The effects of boldness on predation risk may also be weaker in systems in which grouping provides an effective post-encounter defence against predators as a result of collective vigilance or the confusion effect, but in which group size is also in a continual state of flux (e.g. fission-fusion societies; Croft *et al.*, 2003; Aplin *et al.*, 2012).

It is also important to note that these predictions may be altered by the specifics of prey anti-predator tactics and the hunting modes used by predators. There is some evidence that post-encounter prey defensive strategies such as collective vigilance are more effective against stalking or ambush predators, which typically take advantage of cover to draw within close range of prey before initiating a surprise attack, but are less critical to the outcome of an attack against predators with an active hunting mode, which prey usually detect well in advance of an attack (Parrish, 1993; Cresswell and Quinn, 2010; although see Krause, Ruxton and Rubenstein, 1998). In contrast, the confusion effect should be an equally effective defence regardless of whether predators engage in lengthy pursuits or use stealth to strike from an ambush location, as long as the strategy of the predator involves targeting an individual prey item (Neill and Cullen, 1973; Parrish, 1993). The relevance of boldness as a predictor of the risk prey are exposed to might therefore depend on an interaction between prey anti-predator adaptations and critical features of the predator's hunting strategy.

6.2.2 Implications of a predation-specific personality trait for prey behaviour

The existence of a predation-specific personality trait (see Chapter 3) has the potential to alter expectations about the cues which prey use to gauge current levels of predation risk. Since uncertainty surrounding current levels of predation risk can induce greater caution in prey, resulting in lost foraging opportunities, prey should focus their attention on cues which minimise uncertainty by providing a reliable indicator of risk (Sih, 1992; Trussell, Matassa and Luttbeg, 2011; Polo, López and Martín, 2011). If the boldness of an individual predator is tightly correlated with its response to prey, coarse-grained cues revealing the presence of a predator might be a relatively accurate indicator of predation risk from the prey's perspective, due to the close association between boldness and encounter rates. In this scenario, observing a nearby predator would signify that an attack is imminent. In contrast, the existence of a predation-specific personality trait implies that a more reliable way for prey to assess risk might be to closely monitor the behaviour of nearby predators, in order to gain additional information on the predator's attack motivation (e.g. through predator inspection; Dugatkin and Godin, 1992; Murphy and Pitcher, 1997). In this instance, paying more attention to the predator's behaviour would enable prey to reduce ambiguity about current levels of predation risk, whereas the value of this strategy would be diminished in a situation in which simply detecting a predator is a strong indicator of an impending attack.

Differences in the reliability of the information available to prey when predators are initially detected may also have consequences for prey escape tactics. If boldness and the response to prey are positively correlated, prey should have a higher chance of encountering predators which are more likely to approach and attack. Since prey should balance the energetic and opportunity costs of fleeing with the degree of risk the predator represents (Ydenberg and Dill, 1986; Cooper and Blumstein, 2015; Blumstein, Sarnia and Cooper, 2016), the optimal response to this type of predator might be to flee shortly after the predator has been seen, or alternatively to cease moving in order to minimise the likelihood of detection by the predator (Broom and Ruxton, 2005; Staudinger *et al.*, 2013). Conversely, if the predator’s response to prey is independent of its boldness, prey should be just as likely to encounter predators at either end of the behavioural continuum describing inter-individual variation in predation-specific personality. In this instance, delaying the decision to flee might allow prey to update its knowledge about the predator. Therefore, in future work it would be valuable to explore whether predation-specific personality variation is a widespread phenomenon, or a product of specific ecological conditions.

The absence of a link between predatory boldness and the risk prey experience also raises questions about the identity of the factors underpinning inter-individual variation in predator behaviour. In the results presented in Chapter 2, the rate at which three-spined sticklebacks attacked conspicuous prey was associated with the tendency of individual fish to attack cryptic prey in other trials. Since inter-individual differences in attack rates were not explained by boldness, one possible explanation for these results was that inter-individual differences in prey detection were underpinned by another unknown factor. While these results must be interpreted cautiously, because the time taken to attack prey was used as a proxy for prey detection, motivational differences are a suitable candidate for such a factor due to the difficulty in controlling for differences in metabolism which may drive hunger levels, and ultimately the motivation to attack prey (Royauté *et al*., 2018). The wider implications of a connection between motivational factors and inter-individual variation in attack rates are likely to depend on the nature of the feedback loops connecting an individual’s state with its response to prey (Luttbeg and Sih, 2010; Sih *et al*., 2015). Positive feedback loops between state and behaviour arise when inter-individual differences in state and behaviour are mutually reinforcing, which helps maintain, and can even amplify, consistent inter-individual variation in behaviour. By contrast, negative feedback loops emerge when the effects of state and behaviour on one another act in opposing directions, promoting the erosion of personality differences (Sih *et al*., 2015). Positive feedback between motivation and the response of predators to their prey might be expected if individuals which attack prey at a higher rate are also physiologically equipped to process larger amounts of food (Biro and Stamps, 2010; Mathot, Dekinga and Piersma, 2017), or if the degree of skill required to successfully handle specific prey types predisposes individuals with prior experience to persist in their efforts to locate and capture these prey (Wolf, Van Doorn and Weissing, 2008; Sih *et al*., 2015). Alternatively, negative feedbacks could emerge when highly motivated individuals eventually become satiated after repeated successful attacks on prey, which may result in a transient reduction in the proportion of time directed towards hunting (Salvanes and Hart, 1998; Nakayama *et al*., 2012). Whether personality differences persist or are suppressed in the face of such short-term fluctuations is currently unclear, and deserves further attention in a predator-prey context. Research addressing this question could shed light on the temporal patterns of risk prey are likely to be exposed to, which has consequences for how prey should balance anti-predator defences with other vital activities (Lima and Bednekoff, 1999; Ferrari, Sih and Chivers, 2009).

6.2.3 Experiments with responsive robotic prey represent a useful approach for studying predator-prey interactions

Predators can potentially counteract prey defences by learning through experience (Kelley and Magurran, 2011), which might in turn select for prey which behave unpredictably to forestall learned adjustments in predator behaviour (Domenici, Blagburn and Bacon, 2011b; Mitchell, 2009). In Chapter 5, I investigated the effects of prey unpredictability on predator behaviour by comparing the response of blue acara cichlids to robot-controlled prey which were programmed to flee in predictable or unpredictable directions, over the course of multiple interactions. While there have been several attempts to study the response of real prey to interactive robotic predators (Swain *et al*., 2012; Polverino *et al*., 2019; Romano *et al*., 2020), the majority of research examining how real predators attack or pursue virtual or robotic prey tends to feature prey which do not respond to the movements or behaviour of the predator (e.g. Ioannou *et al*., 2019; Heathcote *et al*., 2020). The approach presented in Chapter 5 therefore represents a ‘proof-of-principle’ showing that predator behaviour can be productively studied using this experimental system, which could be modified relatively easily by replacing the simple artificial prey items used here with visually realistic models. Additionally, although the experiment reported in Chapter 5 did not demonstrate conclusively that unpredictability impairs the ability of predators to learn to anticipate the prey's escape direction, aspects of the results from this study were consistent with the expected impact of unpredictability on predator behaviour. Whereas fish appeared to adjust their approach speed to the prey's escape angle in the predictable treatment, no such adjustment was evident with unpredictable prey. While it was difficult to determine fully the functional significance of the adjustments in the predator's approach speed, the finding that predators were sensitive to the escape angle of predictable prey fits in with the idea that predators can fine-tune their behaviour following repeated encounters with the same prey types (Croy and Hughes, 1991).

6.3 Challenges and future directions for studies on predator personality and cognition

6.3.1 Linking predator personality variation to more sophisticated measures of predator and prey behaviour

As I discovered in my work on this thesis, a major challenge facing studies on predator personality variation is the difficulty in repeatedly measuring the behavioural traits of individual predators which have direct relevance to predator-prey interactions. Specifically, it is difficult to balance the need to present individual predators with a standardised prey stimulus, allowing behavioural variation to be measured reliably, whilst also preserving a crucial degree of ecological realism. The field study presented in Chapter 3 was designed to address this, by quantifying inter-individual differences in the response of pike cichlids to an enclosed shoal of guppies in the wild, with predators able to move freely, but this approach has its limitations. One such limitation is that it is difficult to assess how inter-individual variation in the response of pike cichlids to the guppy shoal relates to the behaviour of predators during unconstrained interactions with prey, in which behavioural feedback between the predator and prey can take place unimpeded (Murphy and Pitcher, 1997; McGhee, Pintor and Bell, 2013). While the results presented in Chapter 3 indicated that pike cichlids which spent more time near the prey shoal were more motivated to attack, guppies are well known for their tendency to perform predator inspection behaviour (Seghers and Magurran, 1994), which has the effect of inhibiting predatory attacks (Godin and Davis, 1995; Smith and Blumstein, 2010). The constrained nature of the apparatus used in Chapter 3 is likely to have restricted the ability of guppies to inspect predators and perform typical evasive responses (Walker *et al.*, 2005). It is therefore difficult to predict precisely how the behavioural variation described in Chapter 3 relates to predator behaviour during natural predator-prey interactions. To obtain a more comprehensive overview of the consequences of predator personality variation, this study should ideally have been supplemented by additional observations of predator-prey interactions in the wild involving the same individual pike cichlids. Although logistically difficult to achieve, it would also have been useful to combine these data with behavioural tests on the same individual pike cichlids conducted in a semi-controlled environment, using the approach outlined in Chapter 4. Integrating field and experimental pool-based behavioural observations in this way would have helped provide additional independent measures of the same behavioural traits (e.g. boldness), which can help substantiate conclusions drawn from studies which measure personality differences using a single test for each trait (Carter *et al.*, 2013).

A sharper focus on fine-scale differences in predator behaviour will also be vital in informing a more comprehensive view of the impact of predator personality variation during interactions with prey. In Chapter 4, I compared predator behaviour to the average behaviour of a prey group over the duration of a trial, as a first step towards quantifying the effects of predator personality differences on prey anti-predator responses. Given that prey routinely respond to the behaviour of nearby predators with elaborate and precisely timed evasive movements (Magurran and Pitcher, 1987; Kent *et al.*, 2019; Romenskyy *et al.*, 2019; Storms *et al.*, 2019), future studies could also extend this work by exploring whether predator personality shapes the magnitude of momentary prey anti-predator responses, which are likely to be missed when prey behaviour is averaged over a lengthy time interval. Concentrating on subtle shifts in prey behaviour over the course of a trial might also shed light on whether the personality of the predator influences the extent to which elevated anti-predator responses persist after an attack or a period of high risk, and are carried over into periods when the predator has moved away or has transitioned to a non-threatening state.

More broadly when considering research on predator-prey interactions, relatively few studies have integrated repeated behavioural observations of individual predators with data on their use of hunting strategies in the wild. Although substantial progress has been made by studying the links between personality variation and the movements and search strategies of predators over large spatial scales (van Overveld and Matthysen, 2013; Patrick and Weimerskirch, 2014; Nakayama, Rapp and Arlinghaus, 2016; Patrick, Pinaud and Weimerskirch, 2017), few studies have examined in detail how predator personality affects interactions with behaviourally responsive prey (for an exception, albeit in the laboratory, see McGhee, Pintor and Bell, 2013). Within predator populations, individuals differ in the strategies they use to stalk, attack and capture prey (Kohda, 1994), and it is also common for individuals to switch between different tactics (Savino and Stein, 1989; Cresswell and Quinn, 2010; Brighton *et al*., 2020), but little is currently known about whether personality variation underpins these differences or indeed whether personalities bias individuals towards persisting with particular strategies. Additional field observations might initially provide the best route towards addressing this knowledge gap. Under controlled conditions, spatial constraints can limit the behavioural options available to both predators and prey, and the perception and salience of important cues can also be substantially altered in a laboratory environment. These concerns can be particularly significant in aquatic habitats, in which turbidity, dynamic lighting conditions and the intricacies of water flow can influence how predators respond to cues from prey and *vice versa* (Weissburg, Smee and Ferner, 2014; Chamberlain and Ioannou, 2019; Matchette *et al*., 2020). It can therefore be difficult to replicate key features of complex natural habitats in the laboratory. These difficulties can potentially bias our view of the hunting strategies individual predators adopt in the wild, and how the tactics deployed by predators ultimately relate to prey capture success under varying environmental conditions.

Despite the value of field observations, in many predator-prey systems, interactions between predators and prey are not easy to observe in the wild due to the intermittent nature of predation events. One way to address this problem might be to install hidden camera traps at likely kill sites within a predator's home range, with the aim of documenting patterns of predator activity and the use of specific strategies (Smith *et al*., 2020b). If individuals can be readily identified in the field, observational data obtained in this way could potentially be integrated with personality tests, conducted either in the field or on individuals temporarily taken into captivity. The use of remote cameras could also be extended to monitor the response of individual predators to standardised prey stimuli, including realistic prey models. This could enable aspects of the prey's appearance to be experimentally manipulated, such as colouration or prey posture, which can indicate aspects of the prey's behavioural state, such as its alertness to nearby threats (Krause and Godin, 1995; Cresswell *et al*., 2003). This general approach could be used to test whether personality influences the tendency of individual predators to attack certain prey types, including whether bold predators are relatively impervious to variation in prey defences when deciding to attack, compared to shy individuals which are expected to be more sensitive (Sih and Del Giudice, 2012). Adopting this approach across different populations of marked or identifiable individuals could also shed light on whether the personality composition of predator populations alters selection on traits such as warning signals, as a consequence of inter-individual variation in the propensity to attack brightly coloured prey (Exnerová *et al*., 2010), or differences in the ability to generalise previously learned associations to newly encountered prey (Guillette *et al*., 2017; Rönkä *et al*., 2018). Finally, for some predator species, field-based camera arrays can now be used to reconstruct the three-dimensional trajectory of an attacking predator under natural conditions, potentially allowing variation in fine-scale aspects of predator behaviour to be quantified in the wild (Corcoran and Conner, 2017).

6.3.2 Dynamic aspects of predator-prey interactions

Another substantial deficit in our understanding of predator-prey interactions, including the role of personality, continues to be the relative lack of research exploring how predators and prey dynamically co-adjust their behaviour in response to one another (Lima, 2002). One way of addressing these issues experimentally might be to develop further experiments using the robot-controlled prey system described in Chapter 5. A potentially useful feature of this system is that it would allow the prey response to be adjusted over the course of an experiment. For example, instead of repeatedly presenting individual predators with prey which maintain the same strategy from one trial to the next, as was the case in Chapter 5, it would also be possible to programme prey to switch to a different tactic as the experiment progresses, either gradually or abruptly. In the case of the study presented in Chapter 5, this could involve swapping fish between predictable and unpredictable treatments at the midway point of the experiment. Future experiments adopting this approach could potentially be informative, as they might advance our understanding of how predators modify their behaviour in response to changes in prey strategies. Data on the response of predators to their prey could be combined with personality scores for each individual predator, in order to test whether individual predators differ in their capacity to adjust their behaviour flexibly (see Chapter 1, Section 1.3). This general approach could therefore help shed further light on whether the capacity of a predator to circumvent variable prey defences is dependent on its personality type, and whether certain individuals persist with the same strategies for longer, regardless of shifts in prey behaviour.

Another approach to studying dynamic aspects of predator-prey interactions has been to analyse the movements of mobile predators and prey as a behavioural game, in which the tactics deployed by either participant are contingent on the behaviour of their adversaries (Sih, 1984). Several game theoretical models have used this framework to predict the spatial distribution of predators and prey which emerges at equilibrium, representing the point at which neither participant in the game can boost its fitness via a change in strategy (Hugie and Dill, 1994; Sih, 1998; Luttbeg and Sih, 2004). Whereas predators are expected to distribute themselves close to the prey's preferred resources, prey are predicted to be more evenly dispersed over the landscape. This spatial pattern has been observed in small-scale experiments involving freely interacting predators and prey (Sih, 2005; Hammond, Luttbeg and Sih, 2007), as well as some natural predator-prey systems (Wirsing, Heithaus and Dill, 2007). However, since these models generally assume that individuals are unrestricted in their movements and have perfect knowledge of their environment, it could be instructive to explore whether these predictions are altered by the properties of individual predators which constrain movements or information use (Fraker and Luttbeg, 2012), including attributes such as personality. Along these lines, a recent experiment found evidence that predator hunting mode has an impact on the spatial game between freely interacting predators and prey (Luttbeg *et al*., 2019), but the effects of predator and prey personalities on the spatial component of predator-prey dynamics has not yet been investigated empirically in any depth (DiNuzzo and Griffen, 2020). Understanding whether these effects are influential in heterogeneous landscapes, in which habitat features can either enhance the physical separation of predators and prey (Sih, 1984) or enforce high spatial overlap (Smith *et al*., 2019), will be critical in assessing the relative importance of personality in different predator-prey systems.

Additionally, despite extensive research on the many factors influencing prey anti-predator behaviour, surprisingly little is known about how spatial predator-prey dynamics are affected by the interplay between predator hunting strategies and prey anti-predator tactics. If the movement decisions of predators are guided by their spatial memory of the location of prey, game theoretical models predict that prey should attempt to elude predators by moving constantly, resulting in a predator-prey 'shell game' in which prey abandon profitable feeding patches earlier than expected (Mitchell and Lima, 2002; Mitchell, 2009). As prey tend to increase their vigilance swiftly after detecting cues from nearby predators (Lima and Dill, 1990; Middleton *et al*., 2013), they should therefore become harder to capture following an increase in perceived risk, but there is also evidence that prey progressively relax their state of alertness over time when undisturbed (Beauchamp and Ruxton, 2012a). It has therefore been suggested that predators should refrain from repeatedly attacking prey in the same locations, in order to avoid revisiting the same sites before prey vigilance levels have subsided back to levels which make a successful attack feasible (‘fear management’; Brown, Laundré and Gurung, 1999; Laundré, 2010). Ambush predators might also attack unpredictably in an effort to take advantage of the gradual decline in prey vigilance levels which often ensues once prey have arrived at a foraging location, whilst also provoking uncertainty in the prey’s assessment of whether the patch is safe or not (Beauchamp and Ruxton, 2012b). Observations consistent with these complex predator and prey strategies are only starting to emerge (Roth and Lima, 2007, Cresswell and Quinn, 2012; Katz *et al*., 2013; Beauchamp, 2016; Simon, Cherry and Fortin, 2019), but further theoretical and empirical research on this topic is likely to be critical in developing a more complete picture of predator-prey interactions (Lima, 2002). Since behavioural unpredictability seems to be favoured in a game scenario (Mitchell, 2009; Beauchamp and Ruxton, 2012b; Gal, Alpern and Casas, 2015), more research exploring how unpredictability intersects with factors which appear to limit behavioural plasticity, such as animal personality, may also yield insights furthering our understanding of predator and prey behaviour. A deeper appreciation of the links between personality, cognition and the behavioural sophistication of predators is therefore likely to be an important component of a wider research programme, aimed at developing a more realistic and comprehensive picture of predator-prey interactions.

Bibliography

Abrams, P. A. (1986) ‘Adaptive responses of predators to prey and prey to predators: The failure of the arms-race analogy’, *Evolution*, 40(6), pp. 1229–1247.

Alcalay, Y., Scharf, I. and Ovadia, O. (2014) ‘Behavioral repeatability and personality in pit-building antlion larvae under differing environmental contexts’, *Behavioral Ecology and Sociobiology*, 68(12), pp. 1985-1993.

Alcalay, Y., Scharf, I. and Ovadia, O. (2015) ‘Foraging syndromes and trait variation in antlions along a climatic gradient’, *Oecologia*, 178(4), pp. 1093-1103.

Allen, J., Weinrich, M., Hoppitt, W. and Rendell, L. (2013) ‘Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales’, S*cience*, 340(6131), pp. 485-488.

Anholt, B. R. and Werner, E. E. (1995) ‘Interaction between food availability and predation mortality mediated by adaptive behaviour’, *Ecology*, 76(7), pp. 2230-2234.

Aplin, L. M., Farine, D. R., Morand-Ferron, J. and Sheldon, B. C. (2012) ‘Social networks predict patch discovery in a wild population of songbirds’, *Proceedings of the Royal Society B: Biological Sciences*, 279(1745), pp. 4199-4205.

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cole, E. F., Cockburn, A. and Sheldon, B. C. (2013) ‘Individual personalities predict social behaviour in wild networks of great tits (*Parus major*)’, *Ecology Letters*, 16(11), pp. 1365-1372.

Aplin, L. M., Farine, D. R., Mann, R. P. and Sheldon, B. C. (2014) ‘Individual-level personality influences social foraging and collective behaviour in wild birds’, *Proceedings of the Royal Society B: Biological Sciences*, 281(1789), 20141016.

Aplin, L. M. and Morand-Ferron, J. (2017) ‘Stable producer–scrounger dynamics in wild birds: sociability and learning speed covary with scrounging behaviour’, *Proceedings of the Royal Society B: Biological Sciences*, 284(1852), 20162872.

Araújo, M. S., Bolnick, D. I. and Layman, C. A. (2011) ‘The ecological causes of individual specialisation’, *Ecology Letters*, 14(9), pp. 948-958.

Arnott, S. A., Neil, D. M. and Ansell, A. D. (1999) ‘Escape trajectories of the brown shrimp *Crangon crangon*, and a theoretical consideration of initial escape angles from predators’, *Journal of Experimental Biology*, 202(2), pp. 193-209.

Arvidsson, L. K. and Matthysen, E. (2016) ‘Individual differences in foraging decisions: information-gathering strategies or flexibility?’, *Behavioural Ecology*, 27(5), pp. 1353-1361.

Aubier, T. G. and Sherratt, T. N. (2015) ‘Diversity in Müllerian mimicry: The optimal predator sampling strategy explains both local and regional polymorphism in prey’, *Evolution*, 69(11), pp. 2831-2845.

Aubier, T. G. and Sherratt, T. N. (2020) ‘State-dependent decision-making by predators and its consequences for mimicry’, *The American Naturalist*, 196(5), E127-E143.

Austin, P. (2017) ‘A tutorial on multilevel survival analysis: methods, models and applications’, *International Statistical Review*, 85(2), pp. 185–203

Avery, R. A., Mueller, C. F., Smith, J. A. and Bond, D. J. (1987) ‘The movement patterns of lacertid lizards: speed, gait and pauses in *Lacerta vivipara’, Journal of Zoology*, 211(1), pp. 47-63.

Balaban-Feld, J., Mitchell, W. A., Kotler, B. P., Vijayan, S., Tov Elem, L. T., Rosenzweig, M. L. and Abramsky, Z. (2019a) ‘Individual willingness to leave a refuge and trade-off and safety: a test with social fish’, *Proceedings of the Royal Society B: Biological Sciences*, 286(1907), 20190826.

Balaban-Feld, J., Mitchell, W. A., Kotler, B. P., Vijayan, S., Tov Elem, L. T. and Abramsky, Z. (2019b) ‘State-dependent foraging among social fish in a risky environment’, *Oecologia*, 190(1), pp. 37-45.

Ballew, N. G., Mittelbach, G. G. and Scribner, K. T. (2017) ‘Fitness consequences of boldness in juvenile and adult largemouth bass’, *The American Naturalist*, 189(4), pp. 396-406.

Balme, G., Hunter, L. and Slotow, R. (2007) ‘Feeding habitat selection by hunting leopards *Pardus* in a woodland savanna: prey catchability versus abundance’, *Animal Behaviour*, 74(3), pp. 589-598.

Barbosa, M., Deacon, A. E., Janeiro, M. J., Ramnarine, I., Morrissey, M. B. and Magurran, A. E. (2018) ‘Individual variation in reproductive behaviour is linked to temporal heterogeneity in predation risk’, *Proceedings of the Royal Society B: Biological Sciences*, 285(1870), 20171499.

Barnett, C. A., Skelhorn, J., Bateson, M. and Rowe, C. (2012) ‘Educated predators make strategic decisions to eat defended prey according to their toxin content’, *Behavioral Ecology*, 23(2), pp. 418-424.

Barr, D. J., Levy, R., Scheepers, C. and Tily, H. J. (2013) ‘Random effects structure for confirmatory hypothesis testing: keep it maximal’, *Memory and language*, 68(3), pp. 255-278.

Bateman, P. W. and Fleming, P. A. (2014) ‘Switching to Plan B: changes in the escape tactics of two grasshopper species (Acrididae: Orthoptera) in response to repeated predatory approaches’, *Behavioral Ecology and Sociobiology*, 68(3), pp. 457-465.

Baum, J. K. and Worm, B. (2009) ‘Cascading top-down effects of changing oceanic predator abundances’, *Journal of Animal Ecology*, 78(4), pp. 699-714.

Baylis, A. M. M., Orben, R. A., Arnould, J. P. Y., Peters, K., Knox, T., Costa, D. P. and Staniland, I. J. (2015) ‘Diving deeper into individual foraging specializations of a large marine predator, the southern sea lion’, *Oecologia*, 179(4), pp. 1053-1065.

Beatty, C. D. and Franks, D. W. (2012) ‘Discriminative predation: simultaneous and sequential encounter experiments’, *Current Zoology*, 58(4), pp. 649-657.

Beauchamp, G. (2001) ‘Should vigilance always decrease with group size?’, *Behavioral Ecology and Sociobiology*, 51(1), pp. 47–52.

Beauchamp, G. and Ruxton, G. D. (2012a) ‘Vigilance decreases with time at loafing sites in gulls (*Larus* ssp.)’, *Ethology*, 118(8), pp. 733-739.

Beauchamp, G. and Ruxton, G. D. (2012b) ‘Changes in antipredator vigilance over time caused by a war of attrition between predator and prey’, *Behavioral Ecology*, 23(2), pp. 265-270.

Beauchamp, G. (2016) ‘Timing of attacks by a predator at a prey hotspot’, *Behavioral Ecology and Sociobiology*, 70(2), pp. 269-276.

Beckerman, A. P., Uriarte, M. and Schmitz, O. J. (1997) ‘Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain’, *Proceedings of the National Academy of Sciences U.S.A.*, 94(20), pp. 10735–10738.

Bell, M. A. and Foster, S. A. (1994) *The evolutionary biology of the threespine stickleback*. Oxford: Oxford University Press.

Bell, A. M. (2005) ‘Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*)’, *Journal of Evolutionary Biology*, 18(2), pp. 464-473.

Bell, A. M. and Sih, A. (2007) ‘Exposure to predation generates personality in threespined sticklebacks’, *Ecology Letters*, 10(9), pp. 828-834.

Bell, A. M., Hankison, S. J. and Laskowski, K. L. (2009) ‘The repeatability of behaviour: a meta-analysis’, *Animal Behaviour*, 77(4), pp. 771–783.

Belgrad, B. A. and Griffen, B. D. (2016) ‘Predator-prey interactions mediated by prey personality and predator hunting mode’, *Proceedings of the Royal Society B: Biological Sciences*, 283(1828), 20160408.

Bensky, M. K. and Bell, A. M. (2020) ‘Predictors of individual variation in reversal learning performance in three-spined sticklebacks’, *Animal Cognition*, 23(5), pp. 925-938.

Berger-Tal, O. and Kotler, B. P. (2010) ‘State of emergency: behavior of gerbils is affected by the hunger state of their predators’, *Ecology*, 91(2), pp. 593-600.

Bergmüller, R. and Taborsky, M. (2010) ‘Animal personality due to social niche specialisation’, *Trends in Ecology & Evolution*, 25(9), pp. 504-511.

Beukema, J. J. (1968) ‘Predation by the three-spined stickleback (*Gasterosteus aculeatus* L.): the influence of hunger and experience’, *Behaviour*, 31(1-2), pp. 1-126.

Bevan, P. A., Gosetto, I., Jenkins, E. R., Barnes, I. and Ioannou, C. C. (2018) ‘Regulation between personality traits: individual social tendencies modulate whether boldness and leadership are correlated’, *Proceedings of the Royal Society B: Biological Sciences*, 285(1880), 20180829.

Biro, P. A. and Stamps, J. A. (2010) ‘Do consistent individual differences in metabolic rate promote consistent individual differences in behavior?’, *Trends in Ecology & Evolution*, 25(11), pp. 653-659.

Bishop, T. D. and Brown, J. A. (1992) ‘Threat-sensitive foraging by larval threespine sticklebacks (*Gasterosteus aculeatus*)’, *Behavioral Ecology and Sociobiology*, 31(2), pp. 133-138.

Blackenhorn, W. U. and Perner, D. (1994) ‘Heritability and repeatability of behavioural attributes affecting foraging success and fitness in water striders’, *Animal Behaviour*, 48(1), pp. 169-176.

Blaxter, J. H. S. and Fuiman, L. A. (1990) ‘The role of the sensory systems of herring larvae in evading predatory fishes’, *Journal of the Marine Biological Association of the United Kingdom*, 70(2), pp. 413-427.

Blumstein, D. T., Samia, D. S. M. and Cooper, W. E. (2016) ‘Escape behaviour: dynamic decisions and a growing consensus’, *Current Opinion in Behavioural Sciences*, 12, pp. 24-29.

Bolnick, D. I., Svänback, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D. and Forister, M. L. (2003) ‘The ecology of individuals: incidence and implications of individual specialization’, *The American Naturalist*, 51(1), pp. 1-28.

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., Rudolf, V. H. W., Schreiber, S. J., Urban, M. C. and Vasser, D. (2011) 'Why intraspecific trait variation matters in community ecology', *Trends in Ecology & Evolution*, 26(4), pp. 183-192.

Bond, A. B. (2007) 'The evolution of color polymorphism: crypticity, searching images, and apostatic selection', *Annual Review of Ecology, Evolution and Systematics*, 38, pp. 489-514.

Bond, A. B. and Kamil, A. C. (1999) 'Searching image in blue jays: facilitation and interference in sequential priming', *Animal Learning and Behavior*, 27(4), pp. 461-471.

Bond, A. B. and Kamil, A. C. (2002) 'Visual predators select for crypticity and polymorphism in virtual prey', *Nature*, 415(6872), pp. 609-613.

Boon, A. K., Réale, D. and Boutin, S. (2008) 'Personality, habitat use, and their consequences for survival in North American red squirrels *Tamiasciurus hudsonicus*', *Oikos*, 117(9), pp. 1321-1328.

Borg, B., Bornestaf, C., Hellqvist, A., Schmitz, M. and Mayer, I. (2004) 'Mechanisms in the photoperiodic control of reproduction in the stickleback', *Behaviour* 141(11-12), pp. 1521–1530.

Botham, M. S., Kerfoot, C. J., Louca, V. and Krause, J. (2005) 'Predator choice in the field; grouping guppies, *Poecilia reticulata*, receive more attacks', *Behavioral Ecology and Sociobiology*, 59(2), pp. 181-184.

Botham, M. S., Kerfoot, C. J., Louca, V. and Krause, J. (2006) 'The effects of different predator species on antipredator behaviour in the Trinidadian guppy, *Poecilia reticulata*', *Naturwissenschaften*, 93(9), pp. 431-439.

Botham, M. S., Hayward, R. K., Morrell, L. J., Croft, D. P., Ward, J. R., Ramnarine, I. and Krause, J. (2008) 'Risk-sensitive antipredator behavior in the Trinidadian guppy, *Poecilia reticulata', Ecology* 89(11), pp. 3174-3185.

Bouskila, A. and Blumstein, D. T. (1992) 'Rules of thumb for predation hazard assessment: predictions from a dynamic model', *The American Naturalist*, 139(1), pp. 161-176.

Bremner-Harrison, S., Prodohl, P. A. and Elwood, R. W. (2004) 'Behavioural trait assessment as a release criterion: boldness predicts early death in a reintroduction programme of captive-bred swift fox (*Vulpes velox*)', *Animal Conservation*, 7(3), pp. 313-320.

Briffa, M., Sneddon, L. U. and Wilson, A. J. (2015) 'Animal personality as a cause and consequence of contest behaviour', *Biology Letters*, 11(3), 20141007.

Brighton, C. H., Thomas, A. L. R. and Taylor, G. K. (2017) 'Terminal attack trajectories of peregrine falcons are described by the proportional navigation guidance law of missiles', *Proceedings of the National Academy of Sciences U.S.A.*, 114(51), pp. 13495–13500.

Brighton, C. H. and Taylor, G. K. (2019) 'Hawks steer attacks using a guidance system tuned for close pursuit of erratically moving targets', *Nature Communications*, 10, 2462.

Brighton, C. H., Zusi, L., McGowan, K., Kinniry, M., Kloepper, L. N. and Taylor, G. K. (2020) 'Aerial attack strategies of bat-hunting hawks, and the dilution effect of swarming', *bioRxiv*, doi: https://doi.org/10.1101/2020.02.11.942060.

Briolat, E. S., Burdfield-Steel, E. R., Paul, S. C., Rönkä, K. H., Seymoure, B. M., Stankowich, T. and Stuckert, A. M. M. (2018) 'Diversity in warning colouration: selective paradox or the norm?', *Biological Reviews*, 94(2), pp. 388-414.

Brommer, J. E. (2013) 'On between-individual and residual (co)variances in the study of animal personality: are you willing to take the "individual gambit"?', *Behavioral Ecology and Sociobiology*, 67(6), pp. 1027-1032.

Broom, M. and Ruxton. G. D. (2005) 'You can run—or you can hide: optimal strategies for cryptic prey against pursuit predators', *Behavioral Ecology*, 16(3), pp. 534-540.

Brown, G. E. and Chivers, D. P. (2005) 'Learning as an adaptive response to predation' in Barbosa, P. and Castellanos, I. (eds.) *Ecology of predator-prey interactions*. Oxford: Oxford University Press, pp. 34–54.

Brown, G. E., Rive, A. C., Ferrari, M. C. O. and Chivers, D. P. (2006) 'The dynamic nature of antipredator behavior: prey fish integrate threat-sensitive antipredator responses within background levels of predation risk', *Behavioral Ecology and Sociobiology*, 61(1), pp. 9-16.

Brown, G. E., Macnaughton, C. J., Elvidge, C. K., Ramnarine, I. and Godin, J.-G. J. (2009) 'Provenance and threat-sensitive predator avoidance patterns in wild-caught Trinidadian guppies', *Behavioral Ecology and Sociobiology*, 63(5), pp. 699-706.

Brown, J. S., Laundré, J. W. and Gurung, M. (1999) 'The ecology of fear: optimal foraging, game theory, and trophic interactions', *Journal of Mammalogy*, 80(2), pp. 385-399.

Brown, J. S. and Kotler, B. P. (2004) 'Hazardous duty pay and the foraging cost of predation', *Ecology Letters*, 7(10), pp. 999-1014.

Burkholder, D. A., Heithaus, M. R., Fourqurean, J. W., Wirsing, A. and Dill, L. M. (2013) 'Patterns of top-down control in a seagrass ecosystem: could a roving apex predator induce a behaviour-mediated trophic cascade?', *Journal of Animal Ecology*, 82(6), pp. 1192-1202.

Burnham, K. P. and Anderson, D. R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer Science & Business Media.

Carpenter, S. R., Kitchell, J. F., Hodgson, J. R., Cochran, P. A., Elser, J. J., Elser, M. M., Lodge, D. M., Kretchmer, D., He, X. and von Ende, C. N. (1987) 'Regulation of lake primary productivity by food web structure', *Ecology*, 68(6), pp. 1863-1876.

Carpenter, S. R. and Kitchell, J. F. (1987) 'Consumer control of lake productivity', *BioScience*, 38(11), pp. 764-769.

Carter, A. J., Goldizen, A.W. and Tromp, S. A. (2010) 'Agamas exhibit behavioral syndromes: bolder males bask and feed more but may suffer higher predation', *Behavioral Ecology*, 21(3), pp. 655–661.

Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlishaw, G. and Heinsohn, R. (2013) 'Animal personality: what are behavioural ecologists measuring?', *Biological Reviews*, 88(2), pp. 465-475.

Catano, L. B., Rojas, M. C., Malossi, R. J., Peters, J. R., Heithaus, M. R., Fourqurean, J. W. and Burkepile, D. E. (2016) 'Reefscapes of fear: predation risk and reef hetero-geneity interact to shape herbivore foraging behaviour', *Journal of Animal Ecology*, 85(1), pp. 146-156.

Cauchoix, M., Chow, P. K. Y., van Horik, J. O., Atance, C. M., Barbeau, E. J., Barragan-Jason, G., Bize, P., Boussard, A., Buechel, S. D., Cabirol, A., Cauchard, L., Claidière, N., Dalesman, S., Devaud, J. M., Didic, M., Doligez, B., Fagot, J., Fichtel, C., Henke-von der Malsburg, J., Hermer, E., Huber, L., Huebner, F., Kappeler, P. M., Klein, S., Langbein, J., Langley, E. J. G., Lea, S. E. G., Lihoreau, M., Lovlie, H., Matzel, L. D., Nakagawa, S., Nawroth, C., Oesterwind, S., Sauce, B., Smith, E. A., Sorato, E., Tebbich, S., Wallis, L. J., Whiteside, M. A., Wilkinson, A., Chaine, A. S. and Morand-Ferron, J. (2018) ‘The repeatability of cognitive performance: a meta-analysis’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1756), 20170281.

Chamberlain, A. C. and Ioannou, C. C. (2019) ‘Turbidity increases risk perception but constrains collective behaviour during foraging by fish shoals’, *Animal Behaviour*, 156, pp. 129-138.

Chang, C.-C., Ng, P. J. and Li, D. (2017) ‘Aggressive jumping spiders make quicker decisions for preferred prey but not at the cost of accuracy’, *Behavioral Ecology*, 28(2), pp. 479-484.

Chang, C., Teo, H. Y., Norma-Rashid, Y. and Li, D. (2017) ‘Predator personality and prey behavioural predictability jointly determine foraging performance’, *Scientific Reports*, 7, 40734.

Chen, D. S., Van Dykhuizen, G., Hodge, J. and Gilly, W. F. (1996) ‘Ontogeny of copepod predation in juvenile squid (*Loligo opalescens*)’, *Biological Bulletin*, 190(1), pp. 69-81.

Chittka, L., Skorupski, P. and Raine, N. E. (2009) ‘Speed-accuracy tradeoffs in animal decision making’, *Trends in Ecology & Evolution*, 24(7), pp. 400-407.

Chivers, D. P. and Smith, R. J. F. (1994) ‘Fathead minnows, *Pimephales promelas*, acquire predator recognition when alarm substance is associated with the sight of unfamiliar fish’, *Animal Behaviour*, 48(3), pp. 597-605.

Chivers, D. P., Mirza, R. S., Bryer, P. J. and Kiesecker, J. M. (2001) ‘Threat-sensitive predator avoidance by slimy sculpins: understanding the importance of visual versus chemical information’, *Canadian Journal of Zoology*, 79(5), pp. 867-873.

Chouteau, M., Arias, M. and Joron, M. (2016) ‘Warning signals are under positive frequency-dependent selection in nature’, *Proceedings of the National Academy of Sciences U. S. A.*, 113(8), pp. 2164-2169.

Christianson, D. and Creel, S. (2010) ‘A nutritionally mediated risk effect of wolves on elk’, *Ecology*, 91(4), pp. 1184-1191.

Clark, C. W. (1994) ‘Antipredator behavior and the asset-protection principle’, *Behavioral Ecology*, 5(2), pp. 159-170.

Clark, R. (2007) ‘Public information for solitary foragers: timber rattlesnakes use conspecific chemical cues to select ambush sites’, *Behavioral Ecology*, 18(2), pp. 487-490.

Clark, M. E., Wolcott, T. G., Wolcott, D. L. and Hines, A. H. (1999) ‘Intraspecific interference among foraging blue crabs *Callinectes sapidus*: interactive effects of predator density and prey patch distribution’, *Marine Ecology Progress Series*, 178, pp. 69-78.

Clemente, C. J. and Wilson, R. S. (2016) ‘Speed and maneuverability jointly determine escape success: exploring the functional bases of escape performance using simulated games’, *Behavioral Ecology*, 27(1), pp. 45-54.

Clinchy, M., Sheriff, M. J. and Zanette, L. Y. (2012) ‘Predator-induced stress and the ecology of fear’, *Functional Ecology*, 27(1), pp. 56-65.

Cole, E. F. and Quinn, J. L. (2012) ‘Personality and problem-solving performance explain competitive ability in the wild’, *Proceedings of the Royal Society B: Biological Sciences*, 279(1731), pp. 1168-1175.

Combes, S. A., Rundle, D. E., Iwasaki, J. M and Crall, J. D. (2012) ‘Linking biomechanics and ecology through predator-prey interactions: flight performance of dragonflies and their prey’, *Journal of Experimental Biology*, 215(6), pp. 903-913.

Cooper Jr., W. E. (2006) ‘Dynamic risk assessment: prey rapidly adjust flight initiation distance to changes in predator approach speed’, *Ethology*, 112(9), pp. 858-864.

Cooper Jr., W. E. and Frederick, W. G. (2007) ‘Optimal flight initiation distance’, *Journal of Theoretical Biology*, 244(1), pp. 59–67.

Cooper Jr., W. and Blumstein, D. (2015) *Escaping From Predators: An Integrative View of Escape Decisions*. Cambridge: Cambridge University Press.

Coppens, C. M., de Boer, S. F. and Koolhaas, J. M. (2010) ‘Coping styles and behavioural flexibility: towards underlying mechanisms’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), pp. 4021-4028.

Corcoran, A. J., Wagner, R. D. and Conner, W. E. (2013) ‘Optimal predator risk assessment by the sonar-jamming arctiine moth *Bertholdia trigona*’, *PLoS One*, 8(5), e63609.

Corcoran, A. J. and Conner, W. E. (2016) ‘How moths escape bats: predicting outcomes of predator–prey interactions’, *Journal of Experimental Biology*, 219(17), pp. 2704-2715.

Corcoran, A. J. and Conner, W. E. (2017) ‘Predator counteradaptations: stealth echolocation overcomes insect sonar-jamming and evasive-manoeuvring defences’ *Animal Behaviour*, 132, pp. 291-301.

Cote, J., Fogarty, S., Weinersmith, K., Brodin, T. and Sih, A. (2010) ‘Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*)’, *Proceedings of the Royal Society B: Biological Sciences*, 277(1687), pp. 1571-1579.

Couchoux, C. and Cresswell, W. (2012) ‘Personality constraints versus flexible anti-predation behaviours: how important is boldness in risk management of redshanks (*Tringa totanus*) foraging in a natural system?’, *Behavioral Ecology*, 23(2), pp. 290-301.

Courbin, N., Besnard, A., Péron, C., Saraux, C., Fort, J., Perret, S., Tornos, J. and Grémillet, D. (2018) ‘Short-term prey field lability constrains individual specialisation in resource selection and foraging site fidelity in a marine predator’, *Ecology Letters*, 21(7), pp. 1043-1054.

Cresswell, W., Lind, J., Kaby, U., Quinn, J. L. and Jakobsson, S. (2003) ‘Does an opportunistic predator preferentially attack non-vigilant prey?’, *Animal Behaviour*, 66(4), pp. 643-648.

Cresswell, W. and Quinn, J. L. (2004) ‘Faced with a choice, sparrowhawks more often attack the more vulnerable prey group’, *Oikos*, 104(1), pp. 71-76.

Cresswell, W. and Quinn, J. L. (2010) ‘Attack frequency, attack success and choice of prey group for two predators with contrasting hunting strategies’, *Animal Behaviour*, 80(4), pp. 643-648.

Cresswell, W. and Quinn, J. L. (2012) ‘Local prey vulnerability increases with multiple attacks by a predator’, *Oikos*, 121(8), pp. 1328-1334.

Cresswell, W. and Quinn, J. L. (2013) ‘Contrasting risks from different predators change the overall nonlethal effects of predation risk’, *Behavioral Ecology*, 24(4), pp. 871-876.

Croft, D. P., Arrowsmith, B. J., Bielby, J., Skinner, K., White, E., Couzin, I. D., Magurran, A. E., Ramnarine, I. and Krause, J. (2003) ‘Mechanisms underlying shoal composition in the Trinidadian guppy, *Poecilia reticulata*’, *Oikos*, 100(3), pp. 429–438.

Croft, D. P., Morrell, L. J., Wade, A. S., Piyapong, C., Ioannou, C. C., Dyer, D. R. G., Chapman, B. B., Yan, W. and Krause, J. (2006) ‘Predation risk as a driving force for sexual segregation: A cross-population comparison’, *The American Naturalist*, 167(6), pp. 867 - 878.

Croy, M. I. and Hughes, R. N. (1991) ‘The role of learning and memory in the feeding behaviour of the fifteen-spined stickleback, *Spinachia spinachia* L.’, *Animal Behaviour*, 41(1), pp. 149-159.

Csányi, V. (1985) ‘Ethological analysis of predator avoidance by the paradise fish (*Macropodus opercularis* L.): I. Recognition and learning of predators’, *Behaviour*, 92(3-4), pp. 227-240.

Curio, E., Klump, G. and Regelmann, K. (1983) ‘An anti-predator response in the great tit (*Parus major*): is it tuned to predator risk?’, *Oecologia*, 60(1), pp. 83-88.

Curio, E. and Regelmann, K. (1985) ‘The behavioural dynamics of great tits (*Parus major*) approaching a predator’, *Zeitschrift für Tierpsychologie*, 69(1), pp. 3-18.

Dall, S. R. X., Houston, A. I. and McNamara, J. M. (2004) ‘The behavioural ecology of personality: consistent individual differences from an adaptive perspective’, *Ecology Letters*, 7(8), pp. 734-739.

Dall, S. R. X. (2010) ‘Managing risk: the perils of uncertainty’ in Westneat, D. F. and Fox, C. W. (eds.) *Evolutionary behavioral ecology*. Oxford: Oxford University Press, pp. 194-206.

Dall, S. R. X., Bell, A. M., Bolnick, D. I. and Ratnieks, F. L. W. (2012) ‘An evolutionary ecology of individual differences’, *Ecology Letters*, 15(10), pp. 1189-1198.

Dall, S. R. X. and Griffith, S. C. (2014) ‘An empiricist guide to animal personality variation in ecology and evolution’, *Frontiers in Ecology and Evolution*, 2, 3.

Dammhahn, M. and Almeling, L. (2012) ‘Is risk taking during foraging a personality trait? A field test for cross-context consistency in boldness’, *Animal Behaviour*, 84(5), pp. 1131-1139.

Darimont, C. T., Paquet, P. C. and Reimchen, T. E. (2009) ‘Landscape heterogeneity and marine subsidy generate extensive intrapopulation niche diversity in a large terrestrial vertebrate’, *Journal of Animal Ecology*, 78(1), pp. 126–133.

David, M., Auclair, Y. and Cézilly, F. (2011). ‘Personality predicts social dominance in female zebra finches, *Taeniopygia guttata*, in a feeding context’, *Animal Behaviour*, 81(1), pp. 219-224.

Deacon, A. E., Jones, F. A. M. and Magurran, A. E. (2018) ‘Gradients in predation risk in a tropical river system’, *Current Zoology*, 64(2), pp. 213–221.

Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison, M. T., Schweitzer, J. A. and Palkovacs, E. P. (2018) ‘The ecological importance of intraspecific variation’, *Nature Ecology and Evolution*, 2(1), pp. 57-64.

Dhellemmes, F., Finger, J.-S., Laskowski, K., Guttridge, T. L. and Krause, J. (2020) ‘Comparing behavioural syndromes across time and ecological conditions in a free-ranging predator’, *Animal Behaviour*, 162, pp. 23-33.

Diaz-Pauli, B. and Sih, A. (2017) ‘Behavioural responses to human-induced change: why fishing should not be ignored’, *Evolutionary Applications*, 10(3), pp. 231-240.

Dill, L. M. (1974) ‘The escape response of the zebra danio (*Brachydanio rerio*) I. The stimulus for escape’, *Animal Behaviour*, 22(3), pp. 711-722.

Dill, L. M. (1990) ‘Distance-to-cover and the escape decisions of an African cichlid fish, *Melanochromis chipokae*’, *Environmental Biology of Fishes*, 27, pp. 147-152.

Dingemanse, N. J., Wright, J., Kazem, A. J. N., Thomas, D. K., Hickling, R. and Dawnay, N. (2007) ‘Behavioural syndromes differ predictably between 12 populations of three-spined sticklebacks’, *Journal of Animal Ecology*, 76(6), pp. 1128-1138.

Dingemanse, N. J. and Wolf, M. (2010) ‘Recent models for adaptive personality differences: a review’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), pp. 3947-3958.

Dingemanse, N. J., Bouwman, K. M., van de Pol, M., van Overveld, T., Patrick, S. C., Matthysen, E. and Quinn, J. L. (2011) ‘Variation in personality and behavioural plasticity across four populations of the great tit *Parus major*’, *Journal of Animal Ecology*, 81(1), pp. 116-126.

Dingemanse, N. J. and Dochtermann, N. A. (2013) ‘Quantifying individual variation in behaviour: mixed-effect modelling approaches’, *Journal of Animal Ecology*, 82(1), pp. 39-54.

Dingemanse, N. J. and Wolf, M. (2013) ‘Between-individual differences in behavioural plasticity between populations: causes and consequences’, *Animal Behaviour*, 85(5), pp. 1031-1039.

DiNuzzo, E. R. and Griffen, B. D. (2020) ‘The effects of animal personality on the ideal free distribution’, *Proceedings of the Royal Society B: Biological Sciences*, 287(1934), 20201095.

Dochtermann, N. A., Schwab, T. and Sih, A. (2015) ‘The contribution of additive genetic variation to personality variation: heritability of personality’, *Proceedings of the Royal Society B: Biological Sciences*, 282(1798), 20142201.

Domenici, P. (2001) ‘The scaling of locomotor performance in predator-prey encounters: from fish to killer whales’, *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 131(1), pp. 169-182.

Domenici, P. (2002) ‘The visually mediated escape response in fish: predicting prey responsiveness and the locomotor behaviour of predators and prey’, *Marine and Freshwater Behaviour and Physiology*, 35(1-2), pp. 87-110.

Domenici, P., Booth, D., Blagburn, J. M. and Bacon, J. P. (2008) ‘Cockroaches keep predators guessing by using preferred escape trajectories’, *Current Biology*, 18(22), pp. 1792-1796.

Domenici, P., Blagburn, J.M. and Bacon, J.P. (2011a) ‘Animal Escapology II: escape trajectory case studies’, *Journal of Experimental Biology*, 214(15), pp. 2474-2494.

Domenici, P., Blagburn, J.M. and Bacon, J.P. (2011b) ‘Animal Escapology I: theoretical issues and emerging trends in escape trajectories’, *Journal of Experimental Biology*, 214(15), pp. 2463-2473.

Donelan, S. C., Grabowski, J. H. and Trussell, G. C. (2017) ‘Refuge quality impacts the strength of nonconsumptive effects on prey’, *Ecology*, 98(2), pp. 401-411.

Dougherty, L. R. and Guillette, L. M. (2018) ‘Linking personality and cognition: a meta-analysis’, *Philosophical Transactions of the Royal Society B: Biological Sciences,* 373(1756), 20170282.

Dubois, F., Giraldeau, L.-A. and Réale, D. (2012) ‘Frequency-dependent payoffs and sequential decision-making favour consistent tactic use’, *Proceedings of the Royal Society B: Biological Sciences*, 279(1735), pp. 1977-1985.

Duffield, C. and Ioannou, C. C. (2017) ‘Marginal predation: Do encounter or confusion effects explain the targeting of prey group edges?’, *Behavioral Ecology*, 28(5), pp. 1283–1292.

Dugatkin, L. A. and Godin, J.-G. J. (1992) ‘Predator inspection, shoaling and foraging under predation hazard in the Trinidadian guppy, *Poecilia reticulata*’, *Environmental Biology of Fishes*, 34(3), pp. 265-276.

Dugatkin, L. A. and Alfieri, M. S. (2003) ‘Boldness, behavioural inhibition and learning’, *Ethology, Ecology and Evolution*, 15(1), pp. 43-49.

Dukas, R. (2002) ‘Behavioural and ecological consequences of limited attention’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 357(1427), pp. 1539-1547.

Dukas, R. and Kamil, A. C. (2000) ‘The cost of limited attention in blue jays’, *Behavioral Ecology*, 11(5), pp. 502-506.

Dukas, R. and Kamil, A. C. (2001) ‘Limited attention: the constraint underlying search image’, *Behavioral Ecology*, 12(2), pp. 192–199.

Edut, S. and Eilam, D. (2004) ‘Protean behavior under barn-owl attack: voles alternate between freezing and fleeing and spiny mice flee in alternating patterns’, *Behavioural Brain Research*, 155(2), pp. 207-216.

Ehlinger, T. J. (1989) ‘Learning and individual variation in bluegill foraging: habitat-specific techniques’, *Animal Behaviour*, 38(4), pp. 643-658.

Ehlinger, T. J. and Wilson, D. S. (1988) ‘Complex foraging polymorphism in bluegill sunfish’, *Proceedings of the National Academy of Sciences U.S.A.*, 85(6), pp. 1878-1872.

Elliott, K. H., Woo, K., Gaston, A. J., Benvenuti, S., Dall’Antonia, L. and Davoren, G. K. (2008) ‘Seabird foraging behaviour indicates prey type’, *Marine Ecology Progress Series*, 354, pp. 289-303.

Embar, K., Mukherjee, S. and Kotler, B. P. (2014) ‘What do predators really want? The role of gerbil energetic state in determining prey choice by Barn Owls’, *Ecology*, 95(2), pp. 280-285.

Embar, K., Raveh, A., Burns, D. and Kotler, B. P. (2014) ‘To dare or not to dare? Risk management by owls in a predator-prey foraging game’, *Oecologia*, 175(3), pp. 825-834.

Endler, J. A. (1978) ‘A predator’s view of animal color patterns’ in Hecht, M. K., Steere, W. C and Wallace, B. (eds.) *Evolutionary Biology*. Boston: Springer, pp. 319-364.

Endler, J. A. (1980) ‘Natural selection on color patterns in *Poecilia reticulata*’, *Evolution* 34(1), pp. 76-91.

Endler, J. A. (1987) ‘Predation, light intensity and courtship behaviour in *Poecilia reticulata* (Pisces: Poecilidae)’, *Animal Behaviour*, 35(5), pp. 1376-1385.

Endler, J. A. and Mappes, J. (2004) ‘Predator mixes and the conspicuousness of aposematic signals’, *The American Naturalist*, 163(4), pp. 532–547.

Engström-Öst, J. and Lehtiniemi, M. (2004) ‘Threat-sensitive predator avoidance by pike larvae’, *Journal of Fish Biology*, 65(1), pp. 251-261.

Estes, J. A., Riedman, M. L., Staedler, M. M., Tinker, M. T. and Lyon, B. E. (2003) ‘Individual variation in prey selection by sea otters: patterns, causes and implications’, *Journal of Animal Ecology* 71(1), pp. 144-155.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., Shurin, J. B., Sinclair, A. R. E., Soulé, M., Virtanen, R. and Wardle, D. A. (2011) ‘Trophic downgrading of planet earth’, *Science*, 333(6040), pp. 301-306.

Exnerová, A., Svádová, K. H., Fučíková, E., Drent, P. and Štys P. (2010) ‘Personality matters: individual variation in reactions of naive bird predators to aposematic prey’, *Proceedings of the Royal Society B: Biological Sciences*, 277(1682), pp. 723–728.

Fabian, S. T., Sumner, M. E., Wardill, T. J., Rossoni, S. and Gonzalez-Bellido, P. T. (2018) ‘Interception by two predatory fly species is explained by a proportional navigation feedback controller’, *Journal of the Royal Society Interface*, 15(147), 20180466.

Farwell, M. and McLaughlin, R. L. (2009) ‘Alternative foraging tactics and risk taking in brook charr (*Salvelinus fontinalis*)’, *Behavioral Ecology*, 20(5), pp. 913-921.

Favati, A., Leimar, O. and Løvlie, H. (2014) ‘Personality predicts social dominance in male domestic fowl’, *PLoS ONE* 9(7), e103535.

Ferrari, M. C. O., Kapitania-Kwok, T. and Chivers, D. P. (2006) ‘The role of learning in the acquisition responses to predator odours’, *Behavioral Ecology and Sociobiology*, 60(4), pp. 522–527.

Ferrari, M. O. and Chivers, D. P. (2009) ‘Temporal variability, threat-sensitivity and conflicting information about the nature of risk: understanding the dynamics of tadpole antipredator behaviour’, *Animal Behaviour*, 78(1), pp. 11-16.

Ferrari, M. O., Sih, A. and Chivers, D. P. (2009) ‘The paradox of risk allocation: a review and prospectus’, *Animal Behaviour*, 78(3), pp. 579-585.

Firth, J. A., Cole, E. F., Ioannou, C. C., Quinn, J. L., Aplin, L. M., Culina, A., McMahon, K. and Sheldon, B. C. (2018) ‘Personality shapes pair bonding in a wild bird social system’, *Nature Ecology & Evolution*, 2(11), pp. 1696–1699.

Finke, D. L. and Denno, R. F. (2005) ‘Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades’, *Ecology Letters*, 8(1), pp. 1299-1306.

Fisher, D. N., James, A., Rodríguez-Muñoz, R. and Tregenza, T. (2015) ‘Behaviour in captivity predicts some aspects of natural behaviour, but not others, in a wild cricket population’, *Proceedings of the Royal Society B: Biological Sciences*, 282(1809), 20150708.

Foellmer, M. and Khadka, K. (2013) ‘Does personality explain variation in the probability of sexual cannibalism in the orb-web spider *Argiope aurantia*?’, *Behaviour*, 150(14), pp. 1731-1746.

Foster, W. A. and Treherne, J. E. (1981) ‘Evidence for the dilution effect in the selfish herd from fish predation on a marine insect’, *Nature*, 293(5832), pp. 466-467.

Fraker, M. E. and Luttbeg, B. (2012) ‘Predator-prey space use and the spatial distribution of predation events’, *Behaviour*, 149(5), pp. 555-574.

Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N. and Skalski, G. T. (2001) ‘Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration’, *The American Naturalist*, 158(2), pp. 124-135.

Friard, O. and Gamba, M. (2016) ‘BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations’, *Methods in Ecology and Evolution*, 7(11), pp. 1325-1330.

Fuiman, L. A. (1993) ‘Development of predator evasion in Atlantic herring, *Clupea harengus* L.’, *Animal Behaviour*, 45(6), pp. 1101-1116.

Gal, S., Alpern, S. and Casas, J. (2015) ‘Prey should hide more randomly when a predator attacks more persistently’, *Journal of the Royal Society Interface*, 12(113), 20150861.

Galloway, J. A. M., Green, S. D., Stevens, M. and Kelley, L. A. (2020) ‘Finding a signal hidden among noise: how can predators overcome camouflage strategies?’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375(1802), 20190478.

Gende, S. M. and Quinn, T. P. (2004) ‘The relative importance of prey density and social dominance in determining energy intake by bears feeding on Pacific salmon’, *Canadian Journal of Zoology* 82(1), pp. 75-85.

Gendron, R. P. and Staddon, J. E. R. (1983) ‘Searching for cryptic prey: the effect of search rate’, *The American Naturalist*, 121(2), pp. 172-186.

Gendron, R. P. and Staddon, J. E. R. (1984) ‘A laboratory simulation of foraging behavior: the effect of search rate on the probability of detecting prey’, *The American Naturalist*, 124(3), pp. 407-415.

Ghose, K., Horiuchi, T. K., Krishnaprasad, P. S. and Moss, C. F. (2006) ‘Echolocating Bats Use a Nearly Time-Optimal Strategy to Intercept Prey’, *PLoS Biology* 4(5), e108.

Ghose, K., Triblehorn, J. D., Bohn, K., Yager, D. D. and Moss, C. F. (2009) ‘Behavioral responses of big brown bats to dives by praying mantises’, *Journal of Experimental Biology*, 212(5), pp. 693-703.

Giles, N. and Huntingford, F. A. (1984) ‘Predation risk and inter-population variation in anti-predator behaviour in the three-spined stickleback, *Gasterosteus aculeatus* L.’, *Animal Behaviour*, 32(1), pp. 264-275.

Ginnaw, G., Davidson, I. K., Harding, H. R., Simpson, S., Roberts, N. W., Radford, A. N. and Ioannou, C. C. (2020) ‘Effects of multiple stressors on fish shoal collective motion are independent and vary with shoaling metric’, *Animal Behaviour*, 168(11), pp. 7-17.

Godin, J.-G. J. and Smith, S. A. (1988) ‘A fitness cost of foraging in the guppy’, *Nature*, 333(6168), pp. 69-71.

Godin, J.-G. J. and Davis, S. A. (1995) ‘Who dares, benefits: predator approach behaviour in the guppy (*Poecilia reticulata*) deters predator pursuit’, *Proceedings of the Royal Society B: Biological Sciences*, 259(1355), pp. 193-200.

Graham, M. H. (2003) ‘Confronting Multicollinearity in Ecological Multiple Regression’, *Ecology*, 84(11), pp. 2809-2815.

Griffen, B. D., Toscano, B. J. and Gatto, J. (2012) ‘The role of individual behavior type in mediating indirect interactions’, *Ecology*, 93(8), pp. 1935-1943.

Griffin, A. S., Evans, C. S. and Blumstein, D. T. (2001) ‘Learning specificity in acquired predator recognition’, *Animal Behaviour*, 62(3), pp. 577-589.

Griffin, A. S., Guillette, L. M. and Healy, S. D. (2015) ‘Cognition and personality: an analysis of an emerging field’, *Trends in Ecology & Evolution*, 30(4), pp. 207-214.

Greven, S. and Kneib, T. (2010) ‘On the behaviour of marginal and conditional AIC in linear mixed models’, *Biometrika*, 97(4), pp. 773-789.

Guillette, L. M., Reddon, A. R., Hurd, P. L. and Sturdy, C. B. (2009) ‘Exploration of a novel space is associated with individual differences in learning speed in black-capped chickadees, *Poecile atricapillus’*, *Behavioural Processes*, 82(3), pp. 265-270.

Guillette, L. M., Reddon, A. R., Hoeschele, M. and Sturdy, C. B. (2011) ‘Sometimes slower is better: slow-exploring birds are more sensitive to changes in a vocal discrimination task’, *Proceedings of the Royal Society B: Biological Sciences*, 278(1706), pp. 767-773.

Guillette, L. M., Baron, D. M., Sturdy, C. B. and Spetch, M. L. (2017) ‘Fast- and slow-exploring pigeons differ in how they use previously learned rules’, *Behavioural Processes*, 134, pp. 54-62.

Hadfield, J. D. (2010) ‘MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package’, *Journal of Statistical Software*, 33(2), pp. 1-22.

Hämäläinen, L., Mappes, J., Rowland, H. M., Teichmann, M. and Thorogood, R. (2020) ‘Social learning within and across predator species reduces attacks on novel aposematic prey’, *Journal of Animal Ecology* 89(5), pp. 1153-1164.

Hamblin, S., Mathot, K. J., Morand-Ferron, J., Nocera, J. J., Rieucau, G. and Giraldeau, L.-A. (2010) ‘Predator inadvertent social information use favours reduced clumping of its prey’, *Oikos* 119(2), pp. 286-291.

Hammond, J. I., Luttbeg, B. and Sih, A. (2007) ‘Predator and prey space use: dragonflies and tadpoles in an interactive game’, *Ecology*, 88(6), pp. 1525–1535.

Harcourt, J. L., Ang, T. Z., Sweetman, G., Johnstone, R. A. and Manica, A. (2009a) ‘Social feedback and the emergence of leaders and followers’, *Current Biology*, 19(3), pp. 248-252.

Harcourt, J. L., Sweetman, G., Johnstone, R. A. and Manica, A. (2009b) ‘Personality counts: the effect of boldness on shoal choice in three-spined sticklebacks’, *Animal Behaviour*, 77(6), pp. 1501-1505.

Harris, S. M., Descamps, S., Sneddon, L. U., Bertrand, P., Chastel, O. and Patrick, S. C. (2019) ‘Personality predicts foraging site fidelity and trip repeatability in a marine predator’, *Journal of Animal Ecology*, 89(1), pp. 68-79.

Harrison, P. M., Gutowsky, L. F. G., Martins, E. G., Patterson, D. A., Cooke, S. J. and Power, M. (2015) ‘Personality-dependent spatial ecology occurs independently from dispersal in wild burbot (*Lota lota*)’, *Behavioral Ecology*, 26(2), pp. 483-492.

Harrison, P. M., Gutowsky, L. F. G., Martins, E. G., Ward, T. D., Patterson, D. A., Cooke, S. J. and Power, M. (2017) ‘Individual isotopic specializations predict subsequent inter-individual variation in movement in a freshwater fish’, *Ecology* 98(3), pp. 608-615.

Harrison, P. M., Keeler, R. A., Robichaud, D., Mossup, B., Power, M. and Cooke, S. J. (2019) ‘Individual differences exceed species differences in the movements of a river fish community’, *Behavioral Ecology*, 30(5), pp. 1289-1297.

Harrison, X. A. (2014) ‘Using observation-level random effects to model overdispersion in count data in ecology and evolution’, *PeerJ*, *2*, e616.

Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. D., Robinson, B. S., Hodgson, D. J. and Inger, R. (2018) ‘A brief introduction to mixed effects modelling and multi-model inference in ecology’, *PeerJ*, 6, e4794.

Hartig, F. (2020) ‘DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models’, R package version 0.2.7. https://cran.r-project.org/web/packages/DHARMa/.

Härkönen, L., Hyvärinen, P., Paappanen, J. and Vainikka, A. (2014) ‘Explorative behavior increases vulnerability to angling in hatchery-reared brown trout *Salmo trutta*’, *Canadian Journal of Fisheries and Aquatic Sciences*, 71(12), pp. 1900-1909.

Haselsteiner, A. F., Gilbert, C. and Wang, Z. J. (2014) ‘Tiger beetles pursue prey using a proportional control law with a delay of one half-stride’, *Journal of the Royal Society Interface*, 11(95), 20140216.

Heathcote, R. J. P., Troscianko, J., Darden, S. K., Naisbett-Jones, L. C., Laker, P. L., Brown, A. M., Ramnarine, I. W., Walker, J. and Croft, D. P. (2020) ‘A matador-like predator diversion strategy driven by conspicuous colouration in guppies’, *Current Biology*, 30(14), pp. 1-8.

Hebblewhite, M., Merrill, E. H. and McDonald, T. L. (2005) ‘Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk predator-prey system’, *Oikos*, 111(1), pp. 101-111.

Hein, A. M., Altshuler, D. L., Cade, D. E., Liao, J. C., Martin, B. T. and Taylor, G. K. (2020) ‘An algorithmic approach to natural behaviour’, *Current Biology*, 30(11), R663-R675.

Helfman, G. S. (1989) ‘Threat-sensitive predator avoidance in damselfish-trumpetfish interactions’, *Behavioral Ecology and Sociobiology*, 24(1), pp. 47-58.

Heller, R. and Milinski, M. (1979) ‘Optimal foraging of sticklebacks on swarming prey’, *Animal Behaviour*, 27(4), pp. 1127-1141.

Herbert-Read, J. E., Rosén, E., Szorkovszky, A., Ioannou, C. C., Rogell, B., Perna, A., Ramnarine, I. W., Kotrschal, A., Kolm, N., Krause, J. and Sumpter, D. J. T. (2017a) ‘How predation shapes the social interaction rules of shoaling fish’, *Proceedings of the Royal Society B: Biological Sciences*, 284(1861), 20171126.

Herbert-Read, J. E., Ward, A. J. W., Sumpter, D. J. T. and Mann, R. P. (2017b) ‘Escape path complexity and its context-dependency in Pacific blue-eyes (*Pseudomugil signifer*)’, *Journal of Experimental Biology* 220(11), pp. 2076-2081.

Hertel, A. G., Leclerc, M., Warren, D., Pelletier, F., Zedrosser, A. and Mueller, T. (2019) ‘Don’t poke the bear: using tracking data to quantify behavioural syndromes in elusive wildlife’, *Animal Behaviour*, 147, pp. 91-104.

Hemelrijk, C. K. and Hildenbrandt, H. (2008) ‘Self-organized shape and frontal density of fish schools’, *Ethology*, 114(3), pp. 245 - 254.

Higginson, A. D. and Ruxton, G. D. (2015) ‘Foraging mode switching: the importance of prey distribution and foraging currency’, *Animal Behaviour*, 105, pp. 121-137.

Higham, T. E., Day, S. W. and Wainwright, P. C. (2006) ‘Multidimensional analysis of suction feeding performance in fishes: fluid speed, acceleration, strike accuracy and the ingested volume of water’, *Journal of Experimental Biology*, 209(14), pp. 2713-2725.

Higham, T. E. (2007) ‘Feeding, fins and braking maneuvers: locomotion during prey capture in centrarchid fishes’, *Journal of Experimental Biology*, 210(1), pp. 107-117.

Hitchcock, A. C., Chen, T., Connolly, E., Darakananda, K., Jeong, J., Quist, A., Robbins, A. and Ellerby, D. J. (2015) ‘Trade-offs between performance and variability in the escape responses of bluegill sunfish (*Lepomis macrochirus*)’, *Biology Open*, 4, pp. 743-751.

Hoare, D. J., Couzin, I. D., Godin, J.-G. J. and Krause, J. (2004) ‘Context-dependent group size choice in fish’, *Animal Behaviour*, 67(1), pp. 155-164.

Hogan, B. G., Cuthill, I. C. and Scott-Samuel, N. E. (2017) ‘Dazzle camouflage and the confusion effect: the influence of varying speed on target tracking’, *Animal Behaviour*, 123, pp. 349-353.

Houslay, T. M. and Wilson, A. J. (2017) ‘Avoiding the misuse of BLUP in behavioural ecology’, *Behavioral Ecology*, 28(4), pp. 948-952.

Houslay, T. M., Vierbuchen, M., Grimmer, A. J., Young, A. J. and Wilson, A. J. (2018) ‘Testing the stability of behavioural coping style across stress contexts in the Trinidadian guppy’, *Functional Ecology*, 32(2), pp. 424-438.

Houston, A. I. and McNamara, J. M. (1999) *Models of adaptive behaviour*. Cambridge: Cambridge University Press.

Houston, A. I., McNamara, J. M. and Hutchinson, J. M. C. (1993) ‘General results concerning the trade-off between gaining energy and avoiding predation’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 341(1298), pp. 375-397.

Howland, H. C. (1974) ‘Optimal strategies for predator avoidance: The relative impact of speed and manoeuvrability’, *Journal of Theoretical Biology*, 47(2), pp. 333-350.

Huey, R. B. and Pianka, E. R. (1981) ‘Ecological consequences of foraging mode’, *Ecology*, 62(4), pp. 991-999.

Hügel, T. and Goerlitz, H. R. (2019) ‘Species-specific strategies increase unpredictability of escape flight in eared moths’, *Functional Ecology* 33(9), pp. 1674-1683.

Hugie, D. M. and Dill, L. M. (1994) ‘Fish and game: a game theoretic approach to habitat selection by predators and prey’, *Journal of Fish Biology*, 45(sA), pp. 151-169.

Hughes, R. N. and Croy, M. I. (1993) ‘An experimental analysis of frequency-dependent predation (switching) in the 15-spined stickleback, *Spinachia spinachia*’, *Journal of Animal Ecology*, 62(2), pp. 341-352.

Hulthén, K., Chapman, B. B., Nilsson, P. A., Hansson, L. A., Skov, C., Brodersen, J., Vinterstare, J. and Brönmark, C. (2017) ‘A predation cost to bold fish in the wild’, *Scientific Reports*, 7, 1239.

Humphries, D. A. and Driver, P. M. (1970) ‘Protean defence by prey animals’, *Oecologia*, 5(4), pp. 285-302.

Huntingford, F. A. (1976) ‘The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus Aculeatus*’, *Animal Behaviour*, 24(2), pp. 245-260.

Hynes, H. B. N. (1950) ‘The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes’, *Journal of Animal Ecology*, 19(1), pp. 36-58.

Ingram, T. and Burns, Z. D. (2018) ‘Top-down control by an aquatic invertebrate predator increases with temperature but does not depend on individual behavioural type’, *Ecology and Evolution*, 8(16), pp. 8256-8265.

Ioannou, C. C., Payne, M. and Krause, J. (2008) ‘Ecological consequences of the bold-shy continuum: the effect of predator boldness on prey risk’, *Oecologia*, 157(1), pp. 177–182.

Ioannou, C. C., Ruxton, G. D. and Krause, J. (2008) ‘Search rate, attack probability, and the relationship between prey density and prey encounter rate’, *Behavioral Ecology*, 19(4), pp. 842-846.

Ioannou, C. C., Tosh, C. R., Neville, L. and Krause, J. (2008) ‘The confusion effect - from neural networks to reduced predation risk’, *Behavioral Ecology*, 19(1), pp. 126–130.

Ioannou, C. C., Morrell, L. J., Ruxton, G. D. and Krause, J. (2009) ‘The effect of prey density on predators: conspicuousness and attack success are sensitive to spatial scale’, *The American Naturalist*, 173(4), pp. 499-506.

Ioannou, C. C. and Krause, J. (2009) ‘Interactions between background matching and motion during visual detection can explain why cryptic animals keep still’, *Biology Letters*, 5(2), pp. 191–193.

Ioannou, C. C., Guttal, V. and Couzin, I. C. (2012) ‘Predatory fish select for coordinated collective motion in virtual prey’, *Science*, 337(6099), pp. 1212-1215.

Ioannou, C. C. and Dall, S. R. X. (2016) ‘Individuals that are consistent in risk-taking benefit during collective foraging’, *Scientific Reports*, 6, 33991.

Ioannou C. C., Ramnarine, I. W. and Torney, C. J. (2017) ‘High-predation habitats affect the social dynamics of collective exploration in a shoaling fish’, *Science Advances* 3(5), e1602682.

Ioannou, C. C., Rocque, F., Herbert-Read, J. E., Duffield, C. and Firth, J. A. (2019) ‘Predators attacking virtual prey reveal the costs and benefits of leadership’, *Proceedings of the National Academy of Sciences U. S. A.*, 116(18), pp. 8925–8930.

Jackson, A. L., Beauchamp, G., Broom, M. and Ruxton, G. D. (2006) ‘Evolution of anti-predator traits in response to a flexible targeting strategy by predators’, *Proceedings of the Royal Society B: Biological Sciences*, 273(1590), pp. 1055-1062.

Jeschke, J. M., Kopp, M. and Tollrian, R. (2002) 'Predator functional responses: discriminating between handling and digesting prey', *Ecological Monographs*, 72(1), pp. 95-112.

Johannesen, J., Dunn, A. M. and Morrell, L. J. (2012) 'Olfactory cue use by three-spined sticklebacks foraging in turbid water: prey detection or prey location?', *Animal Behaviour*, 84(1), pp. 151-158.

Johansson, J., Turesson, H. and Persson, A. (2004) 'Active selection for large guppies, *Poecilia reticulata*, by the pike cichlid, *Crenicichla saxatilis*', *Oikos*, 105(3), pp. 595-605.

Johnstone, R. A. and Manica, A. (2011) 'Evolution of personality differences in leadership', *Proceedings of the National Academy of Sciences U. S. A.*, 108(20), pp. 8373-8378.

Jolles, J. W., Ostojić, L. and Clayton, N. S. (2013) 'Dominance, pair bonds and boldness determine social-foraging tactics in rooks, *Corvus frugilegus*', *Animal Behaviour* 85(6), pp. 1261-1269.

Jolles, J. W., Briggs, H. D., Araya-Ajoy, Y. G. and Boogert, N. J. (2019) 'Personality, plasticity and predictability in sticklebacks: bold fish are less plastic and more predictable than shy fish', *Animal Behaviour*, 154, pp. 193-202.

Jones, K. A. and Godin, J.-G. J. (2010) 'Are fast explorers slow reactors? Linking personality type and anti-predator behaviour', *Proceedings of the Royal Society B: Biological Sciences*, 277(1681), pp. 625-632.

Jones, K. A., Jackson, A. L. and Ruxton, G. D. (2011) 'Prey jitters; protean behaviour in grouped prey', *Behavioral Ecology*, 22(4), pp. 831–836.

Jones, N. A. R., Webster, M., Newport, C., Templeton, C. N., Schuster, S. and Rendell, L. (2020) 'Cognitive styles: speed-accuracy trade-offs underlie individual differences in archerfish', *Animal Behaviour*, 160, pp. 1-14.

Kane, S. A., Fulton, A. and Rosenthal, L. J. (2015) 'When hawks attack: animal-borne video studies of goshawk pursuit and prey-evasion strategies', *Journal of Experimental Biology*, 218(2), pp. 212-222.

Kareklas, K., Arnott, G., Elwood, R. W. and Holland, R. A. (2016) 'Plasticity varies with boldness in a weakly electric fish', *Frontiers in Zoology*, 13(1), 22.

Kassambra, A., Kosinski, M. and Biecek, P. (2019) 'survminer: drawing survival curves using 'ggplot2'', R package version 0.4.5, https://cran.r-project.org/web/packages/survminer.

Katz, M. W., Abramsky, Z., Kotler, B. P., Rosenzweig, M. L., Alteshtein, O. and Vasserman, G. (2013) 'Optimal foraging of little egrets and their prey in a foraging game', *The American Naturalist*, 181(3), pp. 381-395.

Kauffmann, M. J., Varley, N., Smith, D. W., Stahler, D. R., MacNulty, D. R. and Boyce, M. S. (2007) 'Landscape heterogeneity shapes predation in a newly restored predator-prey system', *Ecology Letters*, 10(8), pp. 690-700.

Kawabata, Y., Akada, H., Shimatani, K., Nishihara, G. N., Kimura, H., Nozomi, N. and Domenici, P. (2020) 'Geometrical model explains multiple preferred escape trajectories of fish', *bioRxiv*, doi: https://doi.org/10.1101/2020.04.27.049833.

Kramer, D. L. and McLaughlin, R. L. (2001) 'The behavioural ecology of intermittent locomotion', *Integrative and Comparative Biology*, 41(2), pp. 137-153.

Kelley, J. L. and Magurran, A. E. (2011) ‘Learned defences and counterdefences in predator–prey interactions’ in Brown, C., Laland, K. and Krause, J. (eds.) *Fish cognition and behavior*. Oxford: Wiley-Blackwell, pp. 36-58.

Kernaléguen, L., Arnould, J. P. Y., Guinet, C. and Cherel, Y. (2015) ‘Determinants of individual foraging specialization in large marine vertebrates, the Antarctic and subantarctic fur seals’, *Journal of Animal Ecology*, 84(4), pp. 1081-1091.

Kent, M. I. A., Herbert-Read, J. E., McDonald, G., Wood, A. J. and Ward, A. J. W. (2019) ‘Fine-scale behavioural adjustments of prey on a continuum of risk’, *Proceedings of the Royal Society B: Biological Sciences*, 286(1903), 20190448.

Kim, S. (2016) ‘Fixed behavioural plasticity in response to predation risk in the three-spined stickleback’, *Animal Behaviour*, 112, pp. 147-152.

Kluen, E. and Brommer, J. E. (2013) ‘Context-specific repeatability of personality traits in a wild bird: a reaction-norm perspective’, *Behavioral Ecology*, 24(3), 650-658.

Knudsen, R., Amundsen, P.A., Primicerio, R., Klemetsen, A. and Sorensen, P. (2007) ‘Contrasting niche-based variation in trophic morphology within Arctic charr populations’, *Evolutionary Ecology Research*, 9, pp. 1005–1021.

Kohda, M. (1994) ‘Individual specialized foraging repertoires in the piscivorous cichlid fish *Lepidiolamprologus profundicola*’, *Animal Behaviour*, 48(5), pp. 1123-1131.

Kokko, H., Mappes, J. and Lindström, L. (2003) ‘Alternative prey can change model-mimic dynamics between parasitism and mutualism’, *Ecology Letters*, 6(12), pp. 1068-1076.

Koolhaas, J. M., de Boer, S. F., Coppens, C. M. and Buwalda, B. (2010) ‘Neuroendocrinology of coping styles: towards understanding the biology of individual variation’, *Frontiers in Neuroendocrinology*, 31(3), pp. 307-321.

Koski, S. E. (2014) ‘Broader horizons for animal personality research’, *Frontiers in Ecology and Evolution*, 2, 70.

Kobler, A., Klefoth, T., Mehner, T. and Arlinghaus, R. (2009) ‘Coexistence of behavioural types in an aquatic top predator: a response to resource limitation?’, *Oecologia*, 161(4), pp. 837-847.

Kralj-Fišer, S. and Schneider, J. M. (2012) ‘Individual behavioural consistency and plasticity in an urban spider’, *Animal Behaviour*, 84(1), pp. 197-204.

Krakauer, D. C. (1995) ‘Groups confuse predators by exploiting perceptual bottlenecks: a connectionist model of the confusion effect’, *Behavioral Ecology and Sociobiology*, 36(6), pp. 421–429.

Kramer, D. L. and Weary, D. M. (1991) ‘Exploration versus exploitation: a field study of time allocation to environmental tracking by foraging chipmunks’, *Animal Behaviour*, 41(3), pp. 443-449.

Krause, J. and Godin, J.-G. J. (1996) ‘Influence of prey foraging posture on flight behavior and predation risk: predators take advantage of unwary prey’, *Behavioral Ecology* 7(3), pp. 264-271.

Krause, J., Ruxton, G. D. and Rubenstein, D. (1998) ‘Is there always an influence of shoal size on predator hunting success?’, *Journal of Fish Biology*, 52(3), pp. 494-501.

Krause, J. and Ruxton, G. D. (2002) *Living in groups*. Oxford: Oxford University Press.

Krebs, J. R., Kacelnik, A. and Taylor, P. (1978) ‘Test of optimal sampling by foraging great tits’, *Nature*, 275(5675), pp. 27-31.

Krebs, J. R. and Inman, A. J. (1992) ‘Learning and foraging: individuals, groups and populations’, *The American Naturalist*, 140(S1), S63-S84.

Krupa, J. J. and Sih, A. (1998) ‘Fishing spiders, green sunfish, and a stream-dwelling water strider: male-female conflict and prey responses to single versus multiple predator environments’, *Oecologia*, 117(1-2), pp. 258-265.

Krüger, L., Pereira, J. M., Paiva, V. H. and Ramos, J. A. (2019). ‘Personality influences foraging of a seabird under contrasting environmental conditions’, *Journal of Experimental Marine Biology and Ecology*, 516, pp. 123-131.

Kurvers, R.H. J. M., van Oers, K., Nolet, B. A., Jonker, R. M., van Wieren, S. E., Prins, H. H. T. and Ydenberg, R. C. (2010a) ‘Personality predicts the use of social information’, *Ecology Letters*, 13(7), pp. 829-837.

Kurvers, R.H. J. M., Prins, H. H. T., van Wieren, S. E., van Oers, K., Nolet, B. A., Ydenberg, R. C. (2010b) ‘The effect of personality on social foraging: shy barnacle geese scrounge more’, *Proceedings of the Royal Society B: Biological Sciences*, 277(1681), pp. 601-608.

Kusch, R. C., Mirza, R. S. and Chivers, D. P. (2004) ‘Making sense of predator scents: investigating the sophistication of predator assessment abilities of fathead minnows’, *Behavioral Ecology and Sociobiology*, 55(6), pp. 551-555.

La Cœur, C., Thibault, M., Pisanu, B., Thibault, S., Chapuis, J.-L. and Baudry, E. (2015) ‘Temporally fluctuating selection on a personality trait in a wild rodent population’, *Behavioral Ecology*, 26(5), pp. 1285-1291.

Landeau, L. and Terborgh, J. (1986) ‘Oddity and the ‘confusion effect’ in predation’, *Animal Behaviour*, 34(5), pp. 1372-1380.

Lang, S. D. J. and Farine, D. R. (2017) ‘A multidimensional framework for studying social predation strategies’, *Nature Ecology & Evolution*, 1(9), pp. 1230-1239.

Langley, C. M., Riley, D. A., Bond, A. B. and Goel, N. (1996) ‘Visual search for natural grains in pigeons (*Columbia livia*): search images and selective attention’, *Journal of Experimental Psychology*, 22(2), pp. 139-151.

Lapiedra, O., Schoener, T. W., Leal, M., Losos, J. B. and Kolbe, J. J. (2018) ‘Predator-driven natural selection on risk-taking behavior in anole lizards’, *Science*, 360(6392), pp. 1017-1020.

Laundré, J. W. (2010) ‘Behavioral response races, predator-prey shell games, ecology of fear, and patch use of pumas and their ungulate prey’, *Ecology*, 91(10), pp. 2995-3007.

Leahy, S. M., McCormick, M. I., Mitchell, M. D. and Ferrari, M. C. O. (2011) ‘To fear or to feed: the effects of turbidity on perception of risk by a marine fish’, *Biology Letters*, 7(6), pp. 811 - 813.

Lima, S. L. (1998) ‘Nonlethal effects in the ecology of predator-prey interactions: what are the ecological effects of anti-predator decision-making?’, *Bioscience*, 48(1), pp. 25–34.

Lima, S. L. (2002) ‘Putting predators back into behavioral predator–prey interactions’, *Trends in Ecology & Evolution*, 17(2), pp. 70–75.

Lima, S. L. and Dill, L. M. (1990) ‘Behavioral decisions made under the risk of predation: a review and prospectus’, *Canadian Journal of Zoology*, 68(4), pp. 619–640.

Lima, S. L. and Bednekoff, P. A. (1999) ‘Temporal variation in danger drives antipredator behaviour: the predation risk allocation hypothesis’, *The American Naturalist*, 153(6), pp. 649-659.

Lind, J. and Cresswell, W. (2005) ‘Determining the fitness consequences of antipredation behavior’, *Behavioral Ecology*, 16(5), pp. 945-956.

Lindström, L., Alatalo, R. V., Lyytinen, A. and Mappes, J. (2001) ‘Strong antiapostatic selection against novel rare aposematic prey’, *Proceedings of the National Academy of Sciences U.S.A.*, 98(16), pp. 9181–9184.

López-Bao, J. V., Palomares, F., Rodríguez, A. and Ferreras, P. (2011) ‘Intraspecific interference influences the use of prey hotspots’, *Oikos*, 120(10), pp. 1489-1496.

Louison, M. J., Adhikari, S., Stein, J. A. and Suski, C. D. (2017) ‘Hormonal responsiveness to stress is negatively associated with vulnerability to angling capture in fish’, *Journal of Experimental Biology*, 220(14), pp. 2529-2535.

Lourenço, R., Penteriani, V., Rabaça, J. E. and Korpimäki, E. (2014) ‘Lethal interactions among vertebrate top predators: a review of concepts, assumptions and terminology’, *Biological Reviews*, 89(2), pp. 270-283.

Luttbeg, B. and Sih, A. (2004) ‘Predator and prey habitat selection games: the effects of how prey balance foraging and predation risk’, *Israel Journal of Zoology*, 50, pp. 233–254.

Luttbeg, B. and Sih, A. (2010) ‘Risk, resources and state-dependent adaptive behavioural syndromes’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), pp. 3977-3990.

Luttbeg, B. and Trussell, G. C. (2013) ‘How the informational environment shapes how prey estimate predation risk and the resulting indirect effects of predators’, *The American Naturalist*, 181(2), pp. 182-194.

Luttbeg, B., Hammond, J. I., Brodin, T. and Sih, A. (2019) ‘Predator hunting modes and predator-prey space games’, *Ethology*, 126(4), pp. 476-485.

Luttbeg, B., Ferrari, M. C. O., Blumstein, D. T. and Chivers, D. P. (2020) ‘Safety cues can give prey more valuable information than danger cues’, *The American Naturalist*, 195(4), pp. 636-648.

MacGregor, H. E. A., Herbert-Read, J. E. and Ioannou, C. C. (2020) ‘Information can explain the dynamics of group order in animal collective behaviour’, *Nature Communications*, 11, 2737.

Magnhagen, C. and Bunnefeld, N. (2009) ‘Express your personality or go along with the group: what determines the behaviour of shoaling perch?’ *Proceedings of the Royal Society B: Biological Sciences*, 276(1671), pp. 3369-3375.

Magurran, A. E. (2005) *Evolutionary ecology: the Trinidadian guppy*. Oxford: Oxford University Press.

Magurran, A. E. and Girling, S. L. (1986) ‘Predator model recognition and response habituation in shoaling minnows’, *Animal Behaviour*, 34(2), pp. 510-518.

Magurran, A. E. and Pitcher, T. J. (1987) ‘Provenance, shoal size and the sociobiology of predator-evasion behaviour in minnow shoals’, *Proceedings of the Royal Society B: Biological Sciences*, 229(1257), pp. 436-465.

Magurran, A. E. and Seghers, B. H. (1990) ‘Population differences in predator recognition and attack cone avoidance in the guppy *Poecilia reticulata*’, *Animal Behaviour*, 40(3), pp. 443-452.

Magurran, A. E. and Seghers, B. H. (1991) ‘Variation in schooling and aggression amongst guppy (*Poecilia reticulata*) populations in Trinidad’, *Behaviour*, 118(3-4), pp. 214-234.

Magurran, A. E., Seghers, B. H., Carvalho, G. R. and Shaw, P. W. (1992) ‘Behavioural consequences of an artificial introduction of guppies (*Poecilia reticulata*) in N. Trinidad: evidence for the evolution of anti-predator behaviour in the wild’, *Proceedings of the Royal Society B: Biological Sciences*, 248(1322), pp. 117-122.

Mamuneas, D., Spence, A. J., Manica, A. and King, A. J. (2015) ‘Bolder stickleback fish make faster decisions, but they are not less accurate’, *Behavioral Ecology*, 26(1), pp. 91-96.

Martín, J., Luque-Larena, J. J. and López, P. (2006) ‘Collective detection in escape response of temporary groups of Iberian green frogs’, *Behavioral Ecology*, 17(2), pp. 222-226.

Matchette, S. R., Cuthill, I. C. and Scott-Samuel, N. E. (2018) ‘Concealment in a dynamic world: dappled light and caustics mask movement’, *Animal Behaviour*, 143, pp. 51-57.

Matchette, S. R., Cuthill, I. C., Cheney, K. L., Marshall, N. J. and Scott-Samuel, N. E. (2020) ‘Underwater caustics disrupt prey detection by a reef fish’, *Proceedings of the Royal Society B: Biological Sciences*, 287(1924), 20192453.

Mathot, K. J., Wright, J., Kempenaers, B. and Dingemanse, N. J. (2012) ‘Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity’, *Oikos*, 121(7), pp. 1009-1020.

Mathot, K. J., Nicolaus, M., Araya-Ajoy, Y. G., Dingemanse, N. J. and Kempenaers, B. (2015) ‘Does metabolic rate predict risk-taking behaviour? A field experiment in a wild passerine bird’, *Functional Ecology*, 29(2), pp. 239-249.

Mathot, K. J., Dekinga, A. and Piersma, T. (2017) ‘An experimental test of state-behaviour feedbacks: gizzard mass and foraging behaviour in red knots’, *Functional Ecology*, 31(5), pp. 1111-1121.

Mattingly, T. H. and Butler, M. J. (1994) ‘Laboratory predation on the Trinidadian guppy: implications for size-selective predation hypothesis and guppy life history evolution’, *Oikos* 69(1), pp. 54-64.

Mazza, V., Jacob, J., Dammhahn, M., Zaccaroni, M. and Eccard, J. A. (2019) ‘Individual variation in cognitive style reflects foraging and anti-predator strategies in a small mammal’, *Scientific Reports*, 9, 10157.

McDonald, N. D., Rands, S. A., Hill, F., Elder, C. and Ioannou, C. C. (2016) ‘Consensus and experience trump leadership, suppressing individual personality during social foraging’, *Science Advances*, 2(9), e1600892.

McGhee, K. E., Pintor, L. M. and Bell., A. M. (2013) ‘Reciprocal behavioral plasticity and behavioral types during predator-prey interactions’, *The American Naturalist*, 182(6), pp. 704–717.

McHenry, M. J., Johansen, J. D., Soto, A. P., Free, B. A., Paley, D. A. and Liao, J. C. (2019) ‘The pursuit strategy of the predatory bluefish (*Pomatomus saltatrix*)’, *Proceedings of the Royal Society B: Biological Sciences*, 286(1897), 20182934.

Merilaita, S., Scott-Samuel, N. E. and Cuthill, I. C. (2017) 'How camouflage works', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1724), 20160341.

Michalko, R. and Pekar, S. (2017) 'The behavioral types of a top predator drives the short-term dynamic of intraguild predation', *The American Naturalist*, 189(3), pp. 242-253.

Michalko, R. and Řežucha, R. (2018) 'Top predator's aggressiveness and meso-predator's risk-aversion additively determine probability of predation', *Behavioral Ecology and Sociobiology*, 72, 105.

Middleton, A. D., Kauffman, M. J., McWhirter, D. E., Jimenez, M. D., Cook, R. C., Cook, J. G., Albeke, S. E., Sawyer, H. and White, P. J. (2013) 'Linking anti-predator behavior to prey demography reveals limited risk effects of an actively hunting carnivore', *Ecology Letters*, 16(8), pp. 1023-1030.

Milinski, M. (1979) 'Can an experienced predator overcome the confusion effect of swarming prey more easily?', *Animal Behaviour*, 27(4), pp. 1122-1126.

Milinski, M. (1984) 'A predator's costs of overcoming the confusion-effect of swarming prey', *Animal Behaviour*, 32(4), pp. 1157-1162.

Milinski, M. and Heller, R. (1978) 'Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.)', *Nature*, 275(5681), pp. 642-644.

Miller, J. R. B., Ament, J. M. and Schmitz, O. J. (2013) 'Fear on the move: predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response', *Journal of Animal Ecology*, 83(1), pp. 214-222.

Miner, J. G. and Stein, R. A. (1996) 'Detection of predators and habitat choice by small bluegills: effects of turbidity and alternative prey', *Transactions of the American Fisheries Society*, 125(1), pp. 97-103.

Mitchell, W. A. and Lima, S. L. (2002) 'Predator-prey shell games: large-scale movement and its implications for decision-making by prey', *Oikos*, 99(2), pp. 249-259.

Mitchell, W. A. (2009) 'Multi-behavioral strategies in a predator-prey game: an evolutionary algorithm analysis', *Oikos*, 118(7), pp. 1073-1083.

Moiron, M., Mathot, K. J. and Dingemanse, N. J. (2016) 'A multi-level approach to quantify speed-accuracy trade-offs in great tits (*Parus major*)', *Behavioral Ecology*, 27(5), pp. 1539-1546.

Moiron, M., Laskowski, K. L. and Niemelä, P. T. (2020) 'Individual differences in behaviour explain variation in survival: a meta-analysis', *Ecology Letters*, 23(2), pp. 399-408.

Møller, A. P., Liang, W. and Samia, D. S. M. (2019) 'Flight initiation distance, color and camouflage', *Current Zoology*, 65(5), pp. 535-540.

Monk, C. T. and Arlinghaus, R. (2017) 'Encountering a bait is necessary but insufficient to explain individual variability in vulnerability to angling in two freshwater benthivorous fish in the wild', *PLoS ONE*, 12(3), e0173989.

Montiglio, P.-O., Dammhahn, M., Messier, G. D. and Réale, D. (2018) 'The pace-of-life syndrome revisited: the role of ecological conditions and natural history on the slow-fast continuum', *Behavioral Ecology and Sociobiology*, 72, 116.

Montoya, J. M., Pimm, S. L. and Sole, R. V. (2006) ‘Ecological networks and their fragility’, *Nature*, 442(7100), pp. 259-264.

Moore, D. F. (2016) *Applied Survival Analysis Using R*. Switzerland: Springer.

Moore, T. Y., Cooper, K. L., Biewener, A. A. and Vasudevan, R. (2017) ‘Unpredictability of escape trajectory explains predator evasion ability and microhabitat preference of desert rodents’**,** *Nature Communications*, 8, 440.

Moran, N. P., Wong, B. B. M. and Thompson, R. M. (2017) ‘Weaving animal temperament into food webs: implications for biodiversity’, *Oikos*, 126(7), pp. 917-930.

Morand-Ferron, J. (2017) ‘Why learn? The adaptive value of associative learning in wild populations’, *Current Opinion in Behavioral Sciences*, 16, pp. 73-79.

Morand-Ferron, J., Yu, G.-W. and Giraldeau, L.-A. (2011) ‘Persistent individual differences in tactic use in a producer–scrounger game are group dependent’, *Animal Behaviour*, 82(4), pp. 811-816.

Morrell, L. J., Ruxton, G. D. and James, R. (2011) ‘Spatial positioning in the selfish herd’, *Behavioral Ecology*, 22(1), pp. 16-22.

Morrell, L. J., Greenwood, L. and Ruxton, G. D. (2015) ‘Consequences of variation in predator attack for the evolution of the selfish herd’, *Evolutionary Ecology*, 29(1), pp. 107-121.

Moya-Laraño, J. (2011) ‘Genetic variation, predator-prey interactions and food web structure’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1569), pp. 1425-1437.

Mukherjee, S. and Heithaus, M. R. (2013) ‘Dangerous prey and daring predators: a review’, *Biological Reviews*, 88(3), pp. 550-563.

Murdoch, W. W., Avery, S. and Smyth, M. E. B. (1975) ‘Switching in predatory fish’, *Ecology*, 56(5), pp. 1094-1105.

Murie, K. A. and Bourdeau, P. E. (2019) ‘Predator identity dominates non-consumptive effects in a disease-impacted rocky shore food web’, *Oecologia*, 191(4), pp. 945-956.

Murphy, K. E. and Pitcher, T. J. (1997) ‘Predator attack motivation influences the inspection behaviour of European minnows’, *Journal of Fish Biology*, 50(2), pp. 407-417.

Nair, A., Nguyen, C. and McHenry, M. J. (2017) ‘A faster escape does not enhance survival in zebrafish larvae’, *Proceedings of the Royal Society B: Biological Sciences*, 284(1852), 20170359.

Nair, A., Changsing, K., Stewart, W. J. and McHenry, M. J. (2017) ‘Fish prey change strategy with direction of a threat’, *Proceedings of the Royal Society B: Biological Sciences*, 284(1857), 20170393.

Nakagawa, S. and Schielzeth, H. (2010) ‘Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists’, *Biological Reviews* 85(4), pp. 935–956.

Nakagawa, S. and Schielzeth, H. (2012) ‘A general and simple method for obtaining R^2 from generalized linear mixed-effects models’, *Methods in Ecology and Evolution*, 4(2), pp. 133-142.

Nakagawa, S., Johnson, P. C. D. and Schielzeth, H. (2017) ‘The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded’, *Journal of the Royal Society Interface*, 14(134), 20170213.

Nakayama, S., Harcourt, J. L., Johnstone, R. A. and Manica, A. (2016) ‘Who directs group movement? Leader effort versus follower preference in stickleback fish of different personality’, *Biology Letters*, 12(5), 20160207.

Nakayama, S., Rapp, T. and Arlinghaus, R. (2016) ‘Fast–slow life history is correlated with individual differences in movements and prey selection in an aquatic predator in the wild’, *Journal of Animal Ecology*, 86(2), pp. 192-201.

Neill, S. R. J. and Cullen, J. M. (1974) ‘Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators’, *Journal of Zoology*, 172(4), pp. 549-569.

Nicolaus, M., Tinbergen, J. M., Bouwman, K. M., Michler, S. P. M., Ubels, R., Both, C., Kempenaers, B. and Dingemanse, N. J. (2012) ‘Experimental evidence for adaptive personalities in a wild passerine bird’, *Proceedings of the Royal Society B: Biological Sciences*, 279(1749), pp. 4885-4892.

Nicolaus, M., Tinbergen, J. M., Ubels, R., Both, C. and Dingemanse, N. J. (2016) ‘Density fluctuations represent a key process maintaining personality variation in a wild passerine bird’, *Ecology Letters*, 19(4), pp. 478-486.

Niemelä, P. T. and Dingemanse, N. J. (2014) ‘Artificial environments and the study of ‘adaptive’ personalities’, *Trends in Ecology & Evolution*, 29(5), pp. 245–247.

Niemelä, P. T. and Dingemanse, N. J. (2017) ‘Individual versus pseudo-repeatability in behaviour: lessons from translocation experiments in a wild insect’, *Journal of Animal Ecology*, 86(5), pp. 1033-1043.

Niemelä, P. T. and Dingemanse, N. J. (2018) ‘On the usage of single measurements in behavioural ecology research on individual differences’, *Animal Behaviour*, 145, pp. 99-105.

Nokelainen, O., Valkonen, J., Lindstedt, C. and Mappes, J. (2014) ‘Changes in predator community structure shifts the efficacy of two warning signals in Arctiid moths’, *Journal of Animal Ecology*, 83(3), pp. 598–605.

Nøttestad, L., Fernö, A., Mackinson, S., Pitcher, T. and Misund, O. A. (2002) ‘How whales influence herring school dynamics in a cold-front area of the Norwegian Sea’, *ICES Journal of Marine Science* 59(2), pp. 393-400.

Nyqvist, M. J., Gozlan, R. E., Cucherousset, J. and Britton, J. R. (2012) ‘Behavioural syndrome in a solitary predator is independent of body size and growth rate’, *PLoS ONE*, 7(2), e31619.

O’Gorman, E. J. and Emmerson, M. C. (2009) ‘Perturbations to trophic interactions and the stability of complex food webs’, *Proceedings of the National Academy of Sciences U. S. A.*, 106(32), pp. 13393-13398.

Okuyama, T. (2008) ‘Individual behavioral variation in predator–prey models’, *Ecological Research*, 23, pp. 665–671.

Ólafsdóttir, G. A. and Magellan, K. (2016) ‘Interactions between boldness, foraging performance and behavioural plasticity across social contexts’, *Behavioral Ecology and Sociobiology*, 70(11), pp. 1879-1889.

Orrock, J. L., Preisser, E. L., Grabowski, J. H. and Trussell, G. C. (2013) ‘The cost of safety: refuges increase the impact of predation risk in aquatic systems’, *Ecology*, 94(3), pp. 573-579.

Oudman, T., Bijleveld, A. I., Kavelaars, M. M., Dekinga, A., Cluderay, J., Piersma, T. and van Gils, J. A. (2016) 'Diet preferences as the cause of individual differences rather than the consequence', *Journal of Animal Ecology*, 85(5), pp. 1378-1388.

Owings, D. H., Coss, R. G., McKernon, D., Rowe, M. P. and Arrowood, P. C. (2001) 'Snake-directed antipredator behavior of rock squirrels (*Spermophilus variegatus*): population differences and snake-species discrimination', *Behaviour*, 138(5), pp. 575-595.

Page, R. A. and Ryan, M. J. (2005) 'Flexibility in assessment of prey cues: frog-eating bats and frog calls', *Proceedings of the Royal Society B: Biological Sciences*, 279(1565), pp. 841-847.

Page, R. A. and Bernal, X. E. (2019). 'The challenge of detecting prey: Private and social information use in predatory bats', *Functional Ecology*, 34(2), pp. 344-363.

Paine, R. T. (1966). 'Food web complexity and species diversity', *The American Naturalist*, 100(910), pp. 65–75.

Parrish, J. K. (1993) 'Comparison of the hunting behaviour of four piscine predators attacking schooling prey', *Ethology*, 95(3), pp. 233-246.

Patrick, S. C., Bearhop, S., Grémillet, D., Lescroël, A., Grecian, W. J., Bodey, T. W., Hamer, K. C., Wakefield, E., Ne Luz, M. and Votier, S. C. (2013) 'Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator', *Oikos*, 123(1), pp. 33-40.

Patrick, S. C. and Weimerskirch, H. (2014) 'Personality, foraging and fitness consequences in a long lived seabird', *PLoS ONE* 9(2), e87269.

Patrick, S. C. and Weimerskirch, H. (2017) 'Reproductive success is driven by local site fidelity despite stronger specialisation by individuals for large-scale habitat preference', *Journal of Animal Ecology*, 86(3), pp. 674-682.

Patrick, S. C., Pinaud, D. and Weimerskirch, H. (2017) 'Boldness predicts an individual's position along an exploration-exploitation foraging trade-off', *Journal of Animal Ecology*, 86(5), pp. 1257-1268.

Pearish, S., Hostert, L. and Bell, A. M. (2013) 'Behavioral type–environment correlations in the field: a study of three-spined stickleback', *Behavioral Ecology and Sociobiology*, 67(5), pp. 765–774.

Peckarsky, B. L. and Cowan, C. A. (1991). 'Consequences of larval intraspecific competition to stonefly growth and fecundity', *Oecologia*, 88(2), pp. 277-288.

Peckarsky, B. L., Abrams, P. A., Bolnick, D. I., Dill, L. M., Grabowski, J. H., Luttbeg, B., Orrock, J. L., Peacor, S. D., Preisser, E. L., Schmitz, O. J. and Trussell, G. J. (2008) 'Revisiting the classics: considering nonconsumptive effects in textbook examples of predator-prey interactions', *Ecology*, 89(9), pp. 2416–25.

Pedersen, E. J., Miller, D. L., Simpson, G. L. and Ross, N. (2019) 'Hierarchical generalised additive models in ecology: an introduction with mgcv', *PeerJ*, 7, e6876.

Penacchio, O., Harris, J. M. and Lovell, P. G. (2017) 'Establishing the behavioural limits for countershaded camouflage', *Scientific Reports*, 7, 13672.

Penry-Williams, I. L., Ioannou, C. C. and Taylor, M. I. (2018) 'The oddity effect drives prey choice but not necessarily attack time', *Ethology*, 124(7), pp. 496-503.

Pettorelli, N., Coulson, T., Durant, S. M. and Gaillard, J. M. (2011) ‘Predation, individual variability and vertebrate population dynamics’, *Oecologia*, 167(2), pp. 305-314.

Pietrewicz, A. T. and Kamil, A. C. (1979) ‘Search image formation in the blue jay (*Cyanocitta cristata*)’, *Science*, 204(4399), pp. 1332-1333.

Pintor, L. M., Sih, A. and Bauer, M. L. (2008) ‘Differences in aggression, activity and boldness between native and introduced populations of invasive crayfish’, *Oikos*, 117(11), pp. 1629-1636.

Pintor, L. M., McGhee, K. E., Roche, D. P. and Bell, A. M. (2014) ‘Individual variation in foraging behavior reveals a trade-off between flexibility and performance of a top predator’, *Behavioral Ecology and Sociobiology*, 68(10), pp. 1711-1722.

Pitcher, T. J. (1980) ‘Some ecological consequences of fish school volumes’, *Freshwater Biology*, 10(6), pp. 539-544.

Pitcher, T. J., Magurran, A. E. and Winfield, I. J. (1982) ‘Fish in larger shoals find food faster’, *Behavioral Ecology and Sociobiology*, 10(2), pp. 149-151.

Pitcher, T. J., Green, D. A. and Magurran, A. E. (1986) ‘Dicing with death: predator inspection behaviour in minnow shoals’, *Journal of Fish Biology*, 28(4), pp. 439-448.

Polo, V., López, P. and Martín, J. (2011) ‘Uncertainty about future predation risk modulates monitoring behaviour from refuges in lizards’, *Behavioral Ecology*, 22(1), pp. 218-223.

Polverino, G., Karakaya, M., Spinello, C., Soman, V. R. and Porfiri, M. (2019) ‘Behavioural and life-history responses of mosquitofish to biologically inspired and interactive robotic predators’, *Journal of the Royal Society Interface*, 16(158), 20190359.

Post, D. M., Palkovacs, E. P., Schielke, E. G. and Dodson, S. I. (2008) ‘Intraspecific variation in a predator affects community structure and cascading trophic interactions’, *Ecology*, 89(7), pp. 2019-2032.

Potier, S., Carpentier, A., Grémillet, D., Leroy, B. and Lescroël, A. (2015) ‘Individual repeatability of foraging behaviour in a marine predator, the great cormorant, *Phalacrocorax carbo*’, *Animal Behaviour*, 103, pp. 83-90.

Preisser, E. L., Bolnick, D. I. and Benard, M. F. (2005) ‘Scared to death? The effects of intimidation and consumption in predator-prey interactions’, *Ecology*, 86(2), pp. 501–509.

Preisser, E. L., Orrock, J. L. and Schmitz, O. J. (2007) ‘Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions’, *Ecology*, 88(11), pp. 2744-2751.

Pruitt, J. N., Riechert, S. E. and Jones, T. C. (2008) ‘Behavioural syndromes and their fitness consequences in a socially polymorphic spider, *Anelosimus studiosus*’, *Animal Behaviour*, 76(3), pp. 871-879.

Pruitt, J. N., Stachowicz, J. J. and Sih, A. (2012) ‘Behavioral types of predator and prey jointly determine prey survival: potential implications for the maintenance of within-species behavioral variation’, *The American Naturalist*, 179(2), pp. 217–227.

Puttlitz, M. H., Chivers, D. P., Kiesecker, J. M. and Blaustein, A. R. (1999) ‘Threat-sensitive predator avoidance by larval pacific treefrogs (Amphibia, Hylidae)’, *Ethology*, 105(5), pp. 449-456.

Quinn, J. L. and Cresswell, W. (2005) ‘Personality, anti-predation behaviour and behavioural plasticity in the chaffinch *Fringilla coelebs*’, *Behaviour*, 142(9-10), pp. 1377-1402.

Quinn, J. L., Cole, E. F., Bates, J., Payne, R. W. and Cresswell, W. (2012) ‘Personality predicts individual responsiveness to the risks of starvation and predation’, *Proceedings of the Royal Society B: Biological Sciences*, 279(1735), pp. 1919-1926.

R Development Core Team (2019) ‘R: A language and environment for statistical computing’, *R Foundation for Statistical Computing*. http://www.R-project.org.

Rands, S. A., Cowlishaw, G., Pettifor, R. A., Rowcliffe, J. M. and Johnstone, R. A. (2003) ‘Spontaneous emergence of leaders and followers in foraging pairs’, *Nature*, 423(6938), pp. 432-434.

Ratcliffe, J. M., Fullard, J. H., Arthur, B. J. and Hoy, R. R. (2011) ‘Adaptive auditory risk assessment in the dogbane tiger moth when pursued by bats’, *Proceedings of the Royal Society B: Biological Sciences*, 278(1704), pp. 364-370.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T. and Dingemanse, N. J. (2007) ‘Integrating animal temperament within ecology and evolution’, *Biological Reviews*, 82(2), pp. 291–318.

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V. and Montiglio, P.-O. (2010) ‘Personality and the emergence of the pace-of-life syndrome concept at the population level’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), pp. 4051-4063.

Recher, H. F. and Recher, J. A. (1968) ‘Comments on the escape of prey from avian predators’, *Ecology*, 49(3), pp. 560-562.

Reid, A. L., Seebacher, F. and Ward, A. J. W. (2010) ‘Learning to hunt: the role of experience in predator success’, *Behaviour*, 147(2), pp. 223-233.

Reznick, D. and Endler, J. A. (1982) ‘The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*)’, *Evolution*, 36(1), pp. 160-177.

Reznick, D., Bryga, H. and Endler, J. A. (1990) ‘Experimentally induced life-history evolution in a natural population’, *Nature*, 346(6282), pp. 357-359.

Richardson, G., Dickinson, P., Burman, O. H. P. and Pike, T. W. (2018) ‘Unpredictable movement as an anti-predator strategy’, *Proceedings of the Royal Society B: Biological Sciences*, 285(1885), 20181112.

Rieucau, G., Boswell, K. M., De Robertis, A., Macaulay, G. J. and Handegard, N. O. (2014) ‘Experimental evidence of threat-sensitive collective avoidance responses in a large wild-caught herring school’, *PLoS One*, 9(1), e86726.

Riechert, S. E. and Hedrick, A. V. (1993) ‘A test for correlations among fitness-linked behavioural traits in the spider *Agelenopsis aperta* (Araneae, Agelinidae)’, *Animal Behaviour*, 46(4), pp. 669-675.

Rhoades, O. K., Lonhart, S. I. and Stachowicz, J. J. (2019) ‘Human-induced reductions in fish predator boldness decrease their predation rates in kelp forests’, *Proceedings of the Royal Society B*: *Biological Sciences,* 286(1900), 20182745.

Robertson, A., McDonald, R. A., Delahay, R. J., Kelly, S. D. and Bearhop, S. (2015) ‘Resource availability affects individual niche variation and its consequences in group-living European badgers *Meles meles*’, *Oecologia*, 178(1), pp. 31-43.

Rodriguez, A., Zhang, H., Klaminder, J., Brodin, T. Andersson, P. L. and Andersson, M. (2017) ‘ToxTrac: A fast and robust software for tracking organisms’, *Methods in Ecology and Evolution*, 9(3), pp. 460-464.

Rodríguez-Prieto, I., Martín, J. and Fernández-Juricic, E. (2010) ‘Habituation to low-risk predators improves body condition in lizards’, *Behavioral Ecology and Sociobiology*, 64(12), pp. 1937-1945.

Romano, D., Elayan, H., Benelli, G. and Stefanini, C. (2020). ‘Together we stand-analyzing schooling behavior in naive newborn guppies through biorobotic predators’, *Journal of Bionic Engineering*, 17(1), pp. 174–184.

Romenskyy, M., Herbert-Read, J. E., Ioannou, C. C., Szorkovszky, A., Ward, A. J. W. and Sumpter, D. J. T. (2019) ‘Quantifying the structure and dynamics of fish shoals under predation threat in three dimensions’, *Behavioral Ecology*, 31(2), pp. 311-321.

Rönkä, K., De Pasqual, C., Mappes, J., Swanne, G. and Rojas Zuluaga, B. (2018) ‘Colour alone matters: no predator generalization among morphs of an aposematic moth’, *Animal Behaviour*, 135, pp. 153-163.

Roth, T. C. and Lima, S. L. (2007) ‘Use of prey hotspots by an avian predator: purposeful unpredictability?’, *The American Naturalist*, 169(2), pp. 264-273.

Rowland, H., Fulford, A. J. and Ruxton, G. D. (2017) ‘Predator learning differences affect the survival of chemically defended prey’, *Animal Behaviour*, 124, pp. 65-74.

Royauté, R. and Pruitt, J. N. (2015) ‘Varying predator personalities generate contrasting prey communities in an agroecosystem’, *Ecology*, 96(11), pp. 2902-2911.

Royauté, R., Berdal, M. A., Garrison, C. R. and Dochtermann, N. A. (2018) Paceless life? A meta-analysis of the pace-of-life syndrome hypothesis. *Behavioral Ecology and Sociobiology*, 72, 64.

Ruxton, G. D., Sherratt, T. N. and Speed, M. P. (2004) *Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry.* Oxford: Oxford University Press.

Säfken, B., Rügamer, D., Kneib, T. and Greven, S. (2018) ‘Conditional model selection in mixed-effects models with cAIC4’, *arXiv*, doi: 1803.05664.

Salvanes, A. G. V. and Hart, P. J. B. (1998) ‘Individual variability in state-dependent feeding behaviour in three-spined sticklebacks’, *Animal Behaviour*, 55(5), pp. 1349-1359.

Savino, J. F. and Stein, R. A. (1982) ‘Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation’, *Transactions of the American Fisheries Society*, 111(3), pp. 255-266.

Savino, J. F. and Stein, R. A. (1989) ‘Behavioural interactions between fish predators and their prey: effects of plant density’, *Animal Behaviour*, 37(2), pp. 311-321.

Schaerf, T. M., Dillingham, P. W. and Ward, A. J. W. (2017) ‘The effects of external cues on individual and collective behaviour in shoaling fish’, *Science Advances* 3(6), e1603201.

Schielzeth, H. and Forstmeier, W. (2009) ‘Conclusions beyond support: overconfident estimates in mixed models’, *Behavioral Ecology*, 20(2), pp. 416-420.

Schielzeth, H., Dingemanse, N. J., Nakagawa, S., Westneat, D. F., Allegue, H., Teplitsky, C., Réale, D., Dochtermann, N., Garamszegi, L. Z. and Araya-Ajoy, Y. G. (2020) ‘Robustness of linear mixed-effects models to violations of distributional assumptions', *Methods in Ecology and Evolution*, 11(9), pp. 1141-1152.

Schirmer, A., Herde, A., Eccard, J. A. and Dammhahn, M. (2019) 'Individuals in space: personality-dependent space use, movement and microhabitat use facilitate individual spatial niche specialization', *Oecologia*, 189(3), pp. 647-660.

Scott-Samuel, N. E., Holmes, G., Baddeley, R. and Cuthill, I. C. (2015) 'Moving in groups: how density and unpredictable motion affect predation risk', *Behavioral Ecology and Sociobiology*, 69(6), pp. 867-872.

Schmitz, O. J., Krivan, V. and Ovadia, O. (2004). 'Trophic cascades: the primacy of trait-mediated indirect interactions', *Ecology Letters*, 7(2), pp. 153–163.

Schmitz, O. J., Hawlena, D. and Trussell, G. C. (2010) 'Predator control of ecosystem nutrient dynamics', *Ecology Letters*, 13(10), pp. 1199-1209.

Schwartz, A. K. and Hendry, A. P. (2010) 'Testing the influence of local forest canopy clearing on phenotypic variation in Trinidadian guppies', *Functional Ecology*, 24(2), pp. 354-364.

Seghers, B. H. (1974) 'Schooling behaviour in the guppy (*Poecilia reticulata*): an evolutionary response to predation', *Evolution*, 28(3), pp. 486-489.

Seghers, B. H. and Magurran, A. E. (1994) 'Predator inspection behaviour covaries with schooling tendency amongst wild guppy, *Poecilia reticulata*, populations in Trinidad', *Behaviour*, 128(1-2), pp. 121-134.

Sergio, F. and Hiraldo, F. (2008) 'Intraguild predation in raptor assemblages: a review', *Ibis*, 150(s1), pp. 132-145.

Sheppard, C. E., Inger, R., McDonald, R., Barker, S., Jackson, A. L., Thompson, F. J., Vitikainen, E. I. K., Cant, M. A. and Marshall, H. H. (2018) 'Intragroup competition predicts individual foraging specialisation in a group-living mammal', *Ecology Letters*, 21(5), pp. 665-673.

Sheriff, M. J., Krebs, C. J. and Boonstra, R. (2009) 'The sensitive hare: sublethal effects of predator stress on reproduction in snowshoe hares', *Journal of Animal Ecology*, 78(6), pp. 1249–1258.

Sheriff, M. J., Peacor, S. D., Hawlena, D. and Thaker, M. (2020). 'Non-consumptive predator effects on prey population size: a dearth of evidence', *Journal of Animal Ecology*, 89(6), pp. 1302-1316.

Sherratt, T. N. (2003) 'State-dependent risk-taking by predators in systems with defended prey', *Oikos*, 103(1), pp. 93-100.

Sherratt, T. N. (2011) 'The optimal sampling strategy for unfamiliar prey', *Evolution*, 65(7), pp. 2014–2025.

Shettleworth, S. J., Krebs, J. R., Stephens, D. W. and Gibbon, J. (1988) 'Tracking a fluctuating environment: a study of sampling', *Animal Behaviour*, 36(1), pp. 87-105.

Shettleworth, S. J. (2011) *Cognition, evolution and behaviour*. New York: Oxford University Press.

Sih, A. (1984) 'The behavioral response race between predator and prey', *The American Naturalist*, 123(1), pp. 143-150.

Sih, A. (1992) 'Prey uncertainty and the balancing of antipredator and feeding needs', *The American Naturalist*, 139(5), pp. 1052-1069.

Sih, A. (1998) ‘Game theory and predator–prey response races’ in Dugatkin, L. A. and Reeve, H. K. (eds.) *Game theory and animal behavior*. New York: Oxford University Press, pp. 221–238.

Sih, A. (2005) ‘Predator–prey space use as an emergent outcome of a behavioral response race’ in Barbosa, P. and Castellanos, I. (eds.) *Ecology of predator-prey interactions*. New York: Oxford University Press, pp. 240–255.

Sih, A. and Bell, A. M. (2008) ‘Insights for behavioral ecology from behavioral syndromes’, *Advances in the Study of Behavior*, 38, pp. 227-281.

Sih, A., Cote, J., Evans, M., Fogarty, S. and Pruitt, J. N. (2012) ‘Ecological implications of behavioural syndromes’, *Ecology Letters*, 15(3), pp. 278–289.

Sih, A. and Del Giudice, M. (2012) ‘Linking behavioural syndromes and cognition: a behavioural ecology perspective’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1603), pp. 2762-2772.

Sih, A., Mathot, K. J., Moirón, M., Montiglio, P.-O., Wolf, M. and Dingemanse, N. J. (2015) ‘Animal personality and state-behaviour feedbacks: a review and guide for empiricists’, *Trends in Ecology & Evolution*, 30(1), pp. 50-60.

Simon, R. N., Cherry, S. G. and Fortin, D. (2019) ‘Complex tactics in a dynamic large herbivore-carnivore spatiotemporal game’, *Oikos*, 128(9), pp. 1318-1328.

Sims, D. W., Witt, M. J., Richardson, A. J., Southall, E. J. and Metcalfe, J. D. (2006) ‘Encounter success of free-ranging marine predator movements across a dynamic prey landscape’, *Proceedings of the Royal Society B: Biological Sciences*, 273(1591), pp. 1195-1201.

Sinervo, B. and Calsbeek, R. (2006) ‘The developmental, physiological, neural, and genetical causes and consequences of frequency-dependent selection in the wild’, *Annual Review of Ecology, Evolution and Systematics*, 37, pp. 581-610.

Skelhorn, J. and Rowe, C. (2016) ‘Cognition and the evolution of camouflage’, *Proceedings of the Royal Society B: Biological Sciences*, 283(1825), 20152890.

Skelhorn, J., Halpin, C. G. and Rowe, C. (2016) ‘Learning about aposematic prey’, *Behavioral Ecology*, 27(4), pp. 955-964.

Smit, J. A. H. and van Oers, K. (2019) ‘Personality types vary in their personal and social information use’, *Animal Behaviour*, 151, pp. 185-193.

Smith, M. E. and Belk, M. C. (2001) ‘Risk assessment in western mosquitofish (*Gambusia affinis*): do multiple cues have additive effects?’, *Behavioral Ecology and Sociobiology*, 51(1), pp. 101-107.

Smith, B. R. and Blumstein, D. T. (2010) ‘Behavioral types as predictors of survival in Trinidadian guppies (*Poecilia reticulata*)’, *Behavioral Ecology*, 21(5), pp. 919-926.

Smith, J. A., Donadio, E., Pauli, J. N., Bidder, O. R. and Middleton, A. D. (2019) ‘Habitat complexity mediates the predator-prey space race’, *Ecology*, 100(7), e02724.

Smith, J. A., Donadio, E., Bidder, O. R., Pauli, J. N., Sheriff, M. J., Perrig, P. L. and Middleton, A. D. (2020a) ‘Where and when to hunt? Decomposing predation success of an ambush carnivore’, *Ecology*, 101(12), e03172.

Smith, J. A., Suraci, J. P., Hunter, J. S., Gaynor, K. M., Keller, C. B., Palmer, M. S., Atkins, J. L., Castañeda, I., Cherry, M. J., Garvey, P. M., Huebner, S. E., Morin, D. J., Teckentrup, L., Weterings, M. J. A. and Beaudrot, L. (2020b) ‘Zooming in on mechanistic predator-prey ecology: integrating camera traps with experimental methods to reveal the drivers of ecological interactions’, *Journal of Animal Ecology*, 89(9), pp. 1997-2012.

Sommer, N. R. and Schmitz, O. J. (2020) ‘Differences in prey personality mediate trophic cascades’, *Ecology and Evolution*, 10(17), pp. 9538-9551.

Soto, A., Stewart, W. J. and McHenry, M. J. (2015) ‘When optimal strategy matters to prey fish’, *Integrative and Comparative Biology*, 55(1), pp. 110-120.

Spiegel, O., Leu, S. T., Sih, A., Godfrey, S. S. and Bull, C. M. (2015) ‘When the going gets tough: behavioural type-dependent space use in the sleepy lizard changes as the season dries’, *Proceedings of the Royal Society B: Biological Sciences*, 282(1819), 20151768.

Spiegel, O., Leu, S. T., Bull, C. M. and Sih, A. (2017) ‘What’s your move? Movement as a link between personality and spatial dynamics in animal populations’, *Ecology Letters*, 20(1), pp. 3-18.

Stamps, J. A. (2016) ‘Individual differences in behavioural plasticities’, *Biological Reviews*, 91(2), pp. 534–567.

Stamps, J. A., Briffa, M. and Biro, P. A. (2012) ‘Unpredictable animals: individual differences in intraindividual variability (IIV)’, *Animal Behaviour*, 83(6), pp. 1325–1334.

Stankowich, T. and Blumstein, D. T. (2005) ‘Fear in animals: a meta-analysis and review of risk assessment’, *Proceedings of the Royal Society B: Biological Sciences*, 272(1581), pp. 2627–2634.

Stankowich, T. and Goss R. G. (2005) ‘Effects of predator behavior and proximity on risk assessment by Columbian black-tailed deer’, *Behavioral Ecology*, 17(2), pp. 246– 254.

Stapley, J**.** (2004) ‘Do mountain log skinks (*Pseudemoia entrecasteauxii*) modify their behaviour in the presence of two predators?’, *Behavioral Ecology and Sociobiology*, 56(2), pp. 185-189.

Start, D. and Gilbert, B. (2017) ‘Predator personality structures prey communities and trophic cascades’, *Ecology Letters*, 20(3), pp. 366–374.

Staudinger, M. D., Buresch, K. C., Mäthger, L. M., Fry, C., McAnulty, S., Ulmer, K. M. and Hanlon, R. T. (2013) ‘Defensive responses of cuttlefish to different teleost predators’, *The Biological Bulletin*, 225(3), pp. 161-174.

Steinhoff, P. O. M., Warfen, B., Voigt, S., Uhl, G. and Dammhahn, M. (2020) ‘Individual differences in risk-taking affect foraging across different landscapes of fear’, *Oikos*, 129(12), pp. 1891-1902.

Stephens, D. W. (1989) ‘Variance and the value of information’, *The American Naturalist*, 134(1), pp. 128-140.

Stephens, D. W. and Krebs, J. R. (1986) *Foraging Theory*. Princeton: Princeton University Press.

Stephens, D. W., Brown, J. S. and Ydenberg, R. C. (eds.) (2007) *Foraging: behaviour and ecology*. Chicago: University of Chicago Press.

Stephenson, J. F., Van Oosterhout, C., Mohammed, R. S. and Cable, J. (2015) ‘Parasites of Trinidadian guppies: evidence for sex- and age-specific trait-mediated indirect effects of predators’, *Ecology*, 96(2), pp. 489-498.

Stoffel, M. A., Nakagawa, S. and Schielzeth, H. (2017) ‘rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models’, *Methods in Ecology and Evolution*, 8(11), pp. 1639–1644.

Storms, R. F., Carere, C., Zoratto, F. and Hemelrijk, C. K. (2019) ‘Complex patterns of collective escape in starling flocks under predation’, *Behavioral Ecology and Sociobiology*, 73(1), 10.

Stuart-Fox, D., Moussalli, A. and Whiting, M. J. (2008) ‘Predator-specific camouflage in chameleons’, *Biology Letters*, 4(4), pp. 326-329.

Stuber, E. F., Araya-Ajoy, Y. G., Mathot, K. J., Mutzel, A., Nicolaus, M., Wijmenga, J. J., Mueller, J. C. and Dingemanse, N. J. (2013) ‘Slow explorers take less risk: A problem of sampling bias in ecological studies’, *Behavioral Ecology*, 24(5), pp. 1092–1098.

Suraci, J. P., Clinchy, M., Dill, L. M., Roberts, D. and Zanette, L. Y. (2016) ‘Fear of large carnivores causes a trophic cascade’, *Nature Communications*, 7, 10698.

Svänback, R. and Bolnick, D. I. (2007) ‘Intraspecific competition drives increased resource use diversity within a natural population’, *Proceedings of the Royal Society B: Biological Sciences*, 274(1611), pp. 839-844.

Swain, D. T., Couzin, I. D. and Leonard, N. E. (2012) ‘Real-time feedback-controlled robotic fish for behavioral experiments with fish schools’, *Proceedings of the IEEE*, 100(1), pp. 150-163.

Szopa-Comley, A. W., Donald, W. G. and Ioannou, C. C. (2020) ‘Predator personality and prey detection: inter-individual variation in responses to cryptic and conspicuous prey’, *Behavioral Ecology and Sociobiology*, 74, 70.

Szopa-Comley, A. W., Duffield, C., Ramnarine, I. W. and Ioannou, C. C. (2020) ‘Predatory behaviour as a personality trait in a wild fish population’, *bioRxiv*, doi: https://doi.org/10.1101/2020.06.19.161968.

Szopa-Comley, A. W., Duffield, C., Ramnarine, I. W. and Ioannou, C. C. (2020) ‘Predatory behaviour as a personality trait in a wild fish population’, *Animal Behaviour*, 170, pp. 51-64.

Templeton, C. N. and Shriner, W. M. (2004) ‘Multiple selection pressures influence Trinidadian guppy (*Poecilia reticulata*) antipredator behavior’, *Behavioral Ecology*, 15(4), pp. 673-678.

Therneau, T. M. (2018) ‘coxme: Mixed Effects Cox Models’, R package version 2.2-7, https://cran.r-project.org/web/packages/coxme.

Therneau, T. M. and Grambsch, P. M. (2000) *Modelling Survival Data: Extending the Cox Model*. New York: Springer-Verlag.

Thorogood, R., Kokko, H. and Mappes, J. (2018) ‘Social transmission of avoidance among predators facilitates the spread of novel prey’, *Nature Ecology & Evolution*, 2(2), pp. 254-261.

Tinker, M. T., Costa, D. P., Estes, J. A. and Wieringa, N. (2007) ‘Individual dietary specialization and dive behaviour in the California sea otter: using archival time-depth data to detect alternative foraging strategies’, *Deep Sea Research Part II Topical Studies in Oceanography*, 54(3), pp. 330-342.

Tinker, M. T., Bentall, G. and Estes, J. A. (2008) ‘Food limitation leads to behavioral diversification and dietary specialization in sea otters’, *Proceedings of the National Academy of Sciences U.S.A.*, 105(2), pp. 560-565.

Tinker, M.T., Mangel, M. and Estes, J.A. (2009) ‘Learning to be different: acquired skills, social learning, frequency dependence, and environmental variation can cause behaviourally mediated foraging specialisations’, *Evolutionary Ecology Research*, 11(6), pp. 841- 869.

Toscano, B. J. and Griffen, B. J. (2014) ‘Trait-mediated functional responses: predator behavioural type mediates prey consumption’ *Journal of Animal Ecology*, 83(6), pp. 1469-1477.

Toscano, B. J., Gownaris, N. J., Heerhartz, S. M. and Monaco, C. J. (2016) ‘Personality, foraging behavior and specialization: integrating behavioral and food web ecology at the individual level’, *Oecologia*, 182(1), pp. 55-69.

Tosh, C. R. (2011) ‘Which conditions promote negative density dependent selection on prey aggregations?’, *Journal of Theoretical Biology*, 281(1), pp. 24-30.

Towner, A. V., Leos-Barajas, V., Langrock, R., Schick, R. S., Smale, M. J., Kaschke, T., Jewell, O. J. D. and Papastamatiou, Y. P. (2016) ‘Sex-specific and individual preferences for hunting strategies in white sharks’, *Functional Ecology*, 30(8), pp. 1397-1407.

Trompf, L. and Brown, C. (2014) ‘Personality affects learning and trade-offs between private and social information in guppies, *Poecilia reticulata*’, *Animal Behaviour*, 88, pp. 99-106.

Troscianko, J., Skelhorn, J. and Stevens, M. (2018) ‘Camouflage strategies interfere differently with observer search images’, *Proceedings of the Royal Society B: Biological Sciences*, 285(1886), 20181386.

Troscianko, J., Wilson-Aggarwal, J., Stevens, M. and Spottiswoode, C. N. (2016) ‘Camouflage predicts survival in ground-nesting birds’, *Scientific Reports*, 6, 19966.

Trussell, G. C., Matassa, C. M. and Luttbeg, B. (2011) ‘The effects of variable predation risk on foraging and growth: less risk is not necessarily better’, *Ecology*, 92(9), pp. 1799-1806.

Turesson, H. and Brönmark, C. (2007) ‘Predator-prey encounter rates in freshwater piscivores: effects of prey density and water transparency’, *Oecologia*, 152(2), pp. 281-290.

Turner, G. F. and Pitcher, T. J. (1986) ‘Attack abatement: a model for group protection by combined avoidance and dilution’, *The American Naturalist*, 128(2), pp. 228-240.

Tutterow, A. M., Hoffman, A. S., Buffington, J. L., Truelock, Z. T. and Peterman, W. E. (2020) Prey-driven behavioral habitat use in a low-energy ambush predator. *bioRxiv*, doi: https://doi.org/10.1101/2020.09.17.301697.

van Oers, K., Drent, P. J., de Goede, P. and van Noordwijk, A. J. (2004) ‘Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities’, *Proceedings of the Royal Society B: Biological Sciences*, 271(1534), pp. 65-73.

van Oers, K., Klunder, M. and Drent, P. J. (2005) ‘Context dependence of personalities: Risk-taking behavior in a social and a nonsocial situation’, *Behavioral Ecology*, 16(4), pp. 716-723.

van Overveld, T. and Matthysen, E. (2010) ‘Personality predicts spatial responses to food manipulations in free-ranging great tits (*Parus major*)’, *Biology Letters*, 6(2), pp. 187-190.

van Overveld, T. and Matthysen, E. (2013) Personality and information gathering in free-ranging great tits. *PLoS ONE*, 8(2), e54199.

Verbeek, M. E. M., Drent, P. J. and Wiepkema, P. R. (1994) ‘Consistent individual differences in early exploratory behaviour of male great tits’, *Animal Behaviour*, 48(5), pp. 1113-1121.

Vermeij, G. (1982) ‘Unsuccessful predation and evolution’, *The American Naturalist*, 120(6), pp. 701-720.

Villegas-Ríos, D., Réale, D., Freitas, C., Moland, E. and Olsen, E. M. (2018) ‘Personalities influence spatial responses to environmental fluctuations in fish’, *Journal of Animal Ecology*, 87(5), pp. 1390-1319.

Walker, J. A., Ghalambor, C. K., Griset, O. L., McKenney, D. and Reznick, D. N. (2005) ‘Do faster starts increase the probability of evading predators?’, *Functional Ecology*, 19(5), pp. 808-815.

Ward, A. J. W., Thomas, P., Hart, P. J. B. and Krause, J. (2004) ‘Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*)’, *Behavioral Ecology and Sociobiology*, 55(6), pp. 561-568.

Ward, A. J. W., Webster, M. M. and Hart, P. J. B. (2006) ‘Intraspecific food competition in fishes,’ *Fish and Fisheries*, 7(4), pp. 231-261.

Webb, P. W. (1982) ‘Avoidance responses of fathead minnow to strikes by four teleost predators’, *Journal of Comparative Physiology*, 147(3), pp. 371-378.

Webb, P. W. (1984) ‘Body and fin form and strike tactics of four teleost predators attacking fathead minnow (*Pimephales promelas*) prey’, *Canadian Journal of Fisheries and Aquatic Sciences*, 41(1), pp. 157-165.

Webb, P. W. and Skadsen, M. J. (1980) ‘Strike tactics of *Esox’*, *Canadian Journal of Zoology*, 58(8), pp. 1462-1469.

Webster, M. M., Atton, N., Ward, A. J. W. and Hart, P. J. B. (2007) ‘Turbidity and foraging rate in threespine sticklebacks: the importance of visual and chemical prey cues’, *Behaviour*, 144(11), pp. 1347-1360.

Webster, M. M., Ward, A. J. W. and Hart, P. J. B. (2009) ‘Individual boldness affects interspecific interactions in sticklebacks’, *Behavioral Ecology and Sociobiology*, 63(4), pp. 511-520.

Webster, M. M. and Ward, A. J. W. (2011) ‘Personality and social context’, *Biological Reviews*, 86(4), pp. 759-773.

Weihs, D. and Webb, P. W. (1984) ‘Optimal avoidance and evasion tactics in predator–prey interactions’, *Journal of Theoretical Biology*, 106(2), pp. 189-206.

Weimerskirch, H., Bertrand, S., Silva, J., Marques, J. C. and Goya, E. (2010) ‘Use of social information in seabirds: compass rafts indicate the heading of food patches,’ *PLoS ONE*, 5(3), e9928.

Weissburg, M., Smee, D. L. and Ferner, M. C. (2014) ‘The sensory ecology of nonconsumptive predator effects’, *The American Naturalist*, 184(2), pp. 141-157.

Werner, E. E., Gilliam, J. F., Hall, D. J. and Mittelbach, G. G. (1983) ‘An experimental test of the effects of predation risk on habitat use in fish’, *Ecology*, 64(6), pp. 1540-1548.

Werner, E. E. and Anholt, B. R. (1993) ‘Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity’, *The American Naturalist*, 142(2), pp. 242-272.

Whitford, M. D., Freymiller, G. A., Higham, T. E. and Clark, R. W. (2019) ‘Determinants of predation success: how to survive an attack from a rattlesnake’, *Functional Ecology*, 33(6), pp. 1099-1109.

Wilson, A. D. M. and McLaughlin, R. L. (2007) ‘Behavioural syndromes in brook charr, *Salvelinus fontinalis*: prey-search in the field corresponds with space use in novel laboratory situations’, *Animal Behaviour*, 74(4), pp. 689-698.

Wilson, A. D. M. and Godin, J.-G. J. (2009) ‘Boldness and behavioural syndromes in the bluegill sunfish, *Lepomis macrochirus*’, *Behavioral Ecology*, 20(2), pp. 231-237.

Wilson, A. D. M. and Godin, J.-G. J. (2010) ‘Boldness and intermittent locomotion in the bluegill sunfish, *Lepomis macrochirus*’, *Behavioral Ecology*, 21(1), pp. 57-62.

Wilson, A. D. M., Binder, T. R., McGrath, K. P., Cooke, S. J. and Godin, J.-G. J. (2011) ‘Capture technique and fish personality: angling targets timid bluegill sunfish, *Lepomis macrochirus*’, *Canadian Journal of Fisheries and Aquatic Sciences*, 68(5), pp. 749–757.

Wilson, A. D. M., Brownscombe, J. W., Sullivan, B., Jain-Schlaepfer, S. and Cooke, S. J. (2015) ‘Does angling technique selectively target fishes based on their behavioural type?’, *PLoS ONE*, 10(8), e0135848.

Wilson, A. J., Grimmer, A. and Rosenthal, G. G. (2013) ‘Causes and consequences of contest outcome: aggressiveness, dominance and growth in the sheepshead swordtail, *Xiphophorus birchmanni*’, *Behavioral Ecology and Sociobiology*, 67(7), pp. 1151-1161.

Wilson, D. S., Coleman, K., Clark, A. B. and Biederman, L. (1993) ‘Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait’, *Journal of Comparative Psychology*, 107(3), pp. 250-260.

Wilson, R. P., Griffiths, I. W., Mills, M. G. L., Carbone, C., Wilson, J. W. and Scantlebury, D. M. (2015) ‘Mass enhances speed but diminishes turn capacity in terrestrial pursuit predators’, *Elife*, 4, e06487.

Winandy, L. and Denoël, M. (2015) ‘The aggressive personality of an introduced fish affects foraging behavior in a polymorphic newt’, *Behavioral Ecology*, 26(6), pp. 1528-1536.

Wirsing, A. J., Heithaus, M. R. and Dill, L. M. (2007) ‘Living on the edge: dugongs prefer to forage in microhabitats that allow escape from rather than avoidance of predators’, *Animal Behaviour*, 74(1), pp. 93-101.

Wirsing, A. J., Heithaus, M. R., Brown, J. S., Kotler, B. P. and Schmitz, O. J. (2020) ‘The context dependence of non-consumptive predator effects’, *Ecology Letters*, doi: 10.1111/ele.13614.

Wolf, M., van Doorn, S., Leimar, O. and Weissing, F. J. (2007) ‘Life-history trade-offs favour the evolution of animal personalities’, *Nature*, 447(7144), pp. 581-584.

Wolf, M., Van Doorn, G. S. and Weissing, F. J. (2008) ‘Evolutionary emergence of responsive and unresponsive personalities’, *Proceedings of the National Academy of Sciences U.S.A*, 105(41), pp. 15825-15830.

Wolf, M., Van Doorn, G. S. and Weissing, F. J. (2011) ‘On the coevolution of social responsiveness and behavioural consistency’, *Proceedings of the Royal Society B: Biological Sciences*, 278(1704), pp. 440-448.

Wolf, M. and Weissing, F. J. (2012) ‘Animal personalities: consequences for ecology and evolution’, *Trends in Ecology & Evolution*, 27(8), pp. 452-461.

Woo, K. J., Elliott, K. H., Davidson, M., Gaston, A. J. and Davoren, G. K. (2008) ‘Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour’, *Journal of Animal Ecology*, 77(6), pp. 1082-1091.

Ydenberg, R. C. and Dill, L. M. (1986) ‘The economics of fleeing from predators’, *Advances in the Study of Behavior*, 16, pp. 229–249.

Zhan, X., Ma, T., Liu, S. and Shimizu, K. (2017) ‘On circular correlation for data on the torus’, *Statistical papers*, 60, pp. 1827-1847.

Zuur, A. F., Ieno, E. N. and Elphick, C. S. (2010) ‘A protocol for data exploration to avoid common statistical problems’, *Methods in Ecology and Evolution*, 1(1), pp. 3-14.

Appendix for Chapter 3

Supplementary Table 1: Locations, habitat characteristics and numbers of individual pike cichlids observed in the river pools included in the study presented in Chapter 3. C1/P overlap refers to individuals recorded over multiple prey treatment presentations and in at least one control presentation, or in multiple prey treatment presentations and multiple control presentations (C2/P overlap). Data from 16 pools were analysed, as in one of the pools (pool 13) no pike cichlids were observed approaching the stimulus, and in another pool (pool 9) there were a large number of pike cichlids which prevented individuals from being reliably identified.

Pool	**Location (latitude, longitude)**	**Canopy openness (%)**	**No. of individuals observed approaching the stimulus in either treatment**	**No. of individuals observed approaching the stimulus over multiple presentations**			
				Control, C	**Prey treatment, P**	**C1/P overlap**	**C2/P overlap**
1	10°42.143′N, 61°19.239′W	11.09	2	0	2	0	0
2	10°42.173′N, 61°19.277′W	8.58	2	2	2	2	2
3	10°42.197′N, 61°19.284′W	8.49	3	1	1	1	0
4	10°42.258′N, 61°19.277′W	64.91	9	2	5	5	2
5	10°42.286′N, 61°19.256′W	0.00	3	3	2	2	2
6	10°42.293′N, 61°19.246′W	54.08	8	1	3	2	1
7	10°41.988′N, 61°19.239′W	26.52	2	1	2	2	1
8	10°41.039′N, 61°19.277′W	70.29	8	0	6	4	0
10	10°41.971′N, 61°19.252′W	63.26	4	2	2	2	1

11	10°41.976’N, 61°19.269’W	52.78	6	3	4	2	2
12	10°42.001’N, 61°19.262’W	22.36	7	0	5	3	1
14	10°42.258’N, 61°19.277’W	41.73	2	0	0	0	0
15	10°41.336’N, 61°19.487’W	10.20	2	1	2	2	1
16	10°42.327’N, 61°19.243’W	12.10	2	1	1	1	1
17	10°42.334’N, 61°19.240’W	3.38	3	2	2	2	2
18	10°42.377’N, 61°19.210’W	2.60	6	5	5	5	5
Totals			**69**	**24**	**44**	**35**	**21**

Supplementary Table 2: Full statistical results for linear and generalised linear mixed-effects models used to analyse data presented in Chapter 3. R^2 values represent the proportion of variance explained by the fixed effect explanatory variables included within a model (Nakagawa and Schielzeth, 2013), and were calculated using the MuMIn package in R. *P*-values were obtained for each fixed effect explanatory variable by comparing the full model to a reduced model lacking the relevant variable, using likelihood ratio tests. N_{obs} and N_{ind} respectively indicate the number of observations and individual pike cichlids analyses were based on.

Model	**Response variable**	**R^2**	**Explanatory variable(s)**	**Estimate**	**S.E.**	**t value**	***P*-value**
Model 1 (Poisson GLMM) N_{obs} = 211 N_{ind} = 69	Time spent near the stimulus	0.302	Stimulus treatment	1.759	0.192	9.173	<0.001
			Presentation number	0.252	0.092	2.730	0.007
			Time of day	-0.248	0.148	-1.681	0.098
			Canopy openness	-0.633	0.207	-3.065	0.009
			Estimate number of pike cichlids per pool	0.395	0.206	1.914	0.064
Model 2 (Poisson GLMM) N_{obs} = 211 N_{ind} = 69	Time spent near the stimulus	0.306	Stimulus treatment	1.636	0.200	8.169	<0.001
			Proportion of previous prey treatment presentations	0.296	0.097	3.045	0.003
			Time of day	-0.304	0.146	-2.085	0.041
			Canopy openness	-0.687	0.204	-3.366	0.005
			Estimated number of pike cichlids per pool	0.460	0.202	2.279	0.030
Model 3 (binomial GLMM) N_{obs} = 133 N_{ind} = 68	Probability of attack (binary variable indicating whether or not the stimulus was attacked during a presentation)	0.886	Time spent near stimulus	6.847	2.043	3.352	<0.001
			Standard body length	1.290	0.435	2.966	<0.001
			Presentation number	-0.433	0.337	-1.286	0.188
			Time of day	0.299	0.342	0.873	0.379
			Canopy openness	0.620	0.589	1.052	0.291

			Estimated number of pike cichlids per pool	-0.394	0.582	-0.677	0.496
Model 4 (binomial GLMM) N_{obs} = 133 N_{ind} = 68	Probability of attack (binary variable indicating whether or not the stimulus was attacked during a presentation)	0.899	Time spent near stimulus	7.327	2.303	3.182	<0.001
			Standard body length	1.296	0.433	2.991	<0.001
			Proportion of previous prey treatment presentations	-0.443	0.354	-1.250	0.198
			Time of day	0.361	0.345	1.048	0.291
			Canopy openness	0.621	0.582	1.068	0.285
			Estimated number of pike cichlids per pool	-0.440	0.581	-0.757	0.445
Model 5 (Poisson GLMM) N_{obs} = 123 N_{ind} = 63	Number of attacks in the first 30 seconds pike cichlids spent near the stimulus	0.263	Time spent near stimulus	0.212	0.079	2.685	0.009
			Standard body length	0.323	0.074	4.378	<0.001
			Presentation number	-0.095	0.065	-1.473	0.141
			Time of day	0.152	0.138	1.101	0.274
			Canopy openness	-0.008	0.201	-0.040	0.968
			Estimated number of pike cichlids per pool	0.158	0.194	0.815	0.421
Model 6 (Poisson GLMM) N_{obs} = 123 N_{ind} = 63	Number of attacks in the first 30 seconds pike cichlids spent near the stimulus	0.260	Time spent near stimulus	0.200	0.079	2.533	0.014
			Standard body length	0.331	0.074	4.466	<0.001
			Proportion of previous prey treatment presentations	-0.120	0.069	-1.746	0.085
			Time of day	0.167	0.137	1.222	0.231
			Canopy openness	-0.008	0.198	-0.041	0.966
			Estimated number of pike cichlids per pool	0.138	0.191	0.716	0.475
Model 7 (Poisson GLMM) N_{obs} = 68 N_{ind} = 68	Time spent near the stimulus during first prey treatment presentation pike cichlid was observed in	0.154	Total number of prey treatment presentations an individual pike cichlid was observed in	0.849	0.245	3.470	<0.001

Model 8 (Poisson GLMM) N_{obs} = 87 N_{ind} = 35	Time spent near the stimulus, prey treatment presentations	0.192	Mean time spent near stimulus across all control presentations	0.099	0.154	0.646	0.514
			Presentation number	0.092	0.099	0.927	0.357
			Time of day	-0.096	0.180	-0.531	0.597
			Canopy cover	-0.597	0.284	-2.102	0.056
			Estimated number of pike cichlids per pool	0.561	0.277	2.023	0.068
Model 9 (Poisson GLMM) N_{obs} = 87 N_{ind} = 35	Time spent near the stimulus, prey treatment presentations	0.192	Time spent near stimulus, during first control treatment presentation in which an individual was observed	-0.03574	0.136	-0.264	0.792
			Presentation number	0.0934	0.010	0.943	0.349
			Time of day	-0.136	0.185	-0.738	0.466
			Canopy cover	-0.630	0.290	-2.172	0.053
			Estimated number of pike cichlids per pool	0.571	0.285	2.001	0.072
Model 10 (Poisson GLMM) N_{obs} = 109 N_{ind} = 44	Time spent near the stimulus, prey treatment presentations	0.206	Whether or not individual was observed in any control presentations (binary variable)	0.628	0.347	1.809	0.071
			Presentation number	0.026	0.004	6.231	<0.001
			Time of day	0.371	0.018	20.886	<0.001
			Canopy cover	-0.142	0.265	-0.536	0.597
			Estimated number of pike cichlids per pool	0.202	0.250	0.806	0.433
Model 11 (Poisson GLMM) N_{obs} = 109 N_{ind} = 44	Time spent near the stimulus, prey treatment presentations	0.197	Whether or not individual was observed in the first control presentation (binary variable)	0.319	0.297	1.074	0.285
			Presentation number	0.026	0.004	6.236	<0.001
			Time of day	0.371	0.018	20.853	<0.001
			Canopy cover	-0.175	0.273	-0.641	0.530

			Estimated number of pike cichlids per pool	0.220	0.259	0.849	0.412