The University of Hull

The oddity effect: applying principles from psychology to an ecological question

This thesis is submitted for the degree of
Doctor of Philosophy, Biological Sciences,
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by

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Candidate's declaration

I declare that the work submitted in this thesis is my own, except where otherwise stated. The work in this thesis involved collaboration with my supervisors, Lesley Morrell and Paul Skarratt.

For all chapters, both Lesley and Paul were involved with the programming of computerised stimuli. For Chapters 4 and 5 Paul created the conditions files containing all the potential variable combinations. For Chapters 3 and 4, Lesley wrote the R function for extracting spatial data from coordinates.

In addition, Chapter 2 has been accepted for publication as:

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At the reviewers request the analysis, which used stepwise removal of non-significant interactions, was changed to an AIC model averaging approach. The analysis presented was carried out by Lesley, but the results and interpretation did not change from the original analysis, which presented p-values. The original approach is retained in the remaining chapters.

I further declare that no part of this work has been submitted as part of any other degree. This copy has been supplied on the understanding that it is copyright material and that no quotation from the thesis may be published without proper acknowledgment.

Khia E. Dobbinson, 2019

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Additional thanks is extended to Lesley who has been the best supervisor I could have hoped for. This is for many reasons, all of which are underpinned by a feeling that my best interests were always in mind.

While I believe that education should be a right the reality is that it is a privilege and I am very fortunate to have had the opportunity to remain in education for as long as I have. I am endlessly grateful to my mum, Sushie, who is responsible for my early and consistent exposure to people and environments that placed a high value on ideas, thought and learning. I am also immensely privileged to have had the security of a roof over my head in the latter (unfunded) stages of this work. I am a very fortunate person to have had that kind of support available to me.

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Summary

Chapter 2 serves as proof of concept for the use of stickleback predators targeting computerised prey groups to study the oddity effect. Stickleback target odd prey-dots more often that would be expected by chance when 1 or 2, but not 3 or 4, odd prey-dots are present within a group of 16. The validity of computerised stimuli for studying oddity effects is demonstrated and a low threshold for preferential targeting of odd prey is observed. In Chapter 3, the methodology established in Chapter 2 is employed to examine how the selection of odd prey is affected by group features associated with the confusion effect. Chapter 3 concludes that it is numerical group size, rather than local density or the area that a group occupies that drives the preferential targeting of odd prey.

Chapter 4 shifts from the attack stage of predation to examine the oddity effect and attentional capture at the detection stage, using human subjects. Chapter 4 demonstrates that oddity captures attention and eases the challenge associated with searching numerically large prey groups. Spatial results suggest that the proximity of group members to odd individuals may affect their risk. However, whether risk is increased or decreased would depend on the predator-prey system in question. In Chapter 5 the focus remains on oddity and attentional capture at the detection stage of predation. Chapter 5 aims to establish when a minority phenotype in a mixed group captures attention in line with the effect of oddity observed in Chapter 4. Here, a higher threshold of oddity is observed than in Chapter 2, with oddity capturing attention at ≤ 4 out of 16 prey-dots.

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Chapter 1. General introduction

In order to maximise fitness, organisms must interact with, and respond to, their environment (Danchin et al., 2008). For the majority of phyla, photoreception is an essential part of their ecology (Land & Nilsson, 2012). Many animals, including humans, go beyond simply detecting light and interact with the world in a meaningful, visual way. True visually mediated behaviour requires organs that provide spatial vision, i.e. the eyes (Land & Nilsson, 2012) and the ability of visual perception. Visual perception is essentially the translation of light energy into an interpretation of the world around us (Snowden et al., 2012). The visual system converts photons of light into neural impulses, the brain then processes and interprets these impulses as meaningful, but subjective, images (Bruce et al., 2003). Visual information is interpreted using physical cues such as colour, depth and texture in addition to more abstract information relating to previous experiences, knowledge and expectations (Bruce et al., 2003; Land & Nilsson, 2012).

An organism with a complex visual system receives a vast amount of visual input but can only attend to a fraction of this. There are a greater number of retinal receptors than axons within the optic nerve of vertebrates (Marc, 1999). This *perceptual bottleneck* (Bingham, 1988, see Box 1 for italicised key terms; Krakauer, 1995) fundamentally limits the capacity of the visual system, with the human retina transmitting data at approximately the rate of an Ethernet connection (Koch et al., 2006). An ability to filter out irrelevant information is necessary to avoid overburdening the sensory systems as there is a limit to the amount of information that can be processed at one time (Barlow, 1961; Verghese & Pelli, 1992). Sensory filtering is achieved by means of *visual attention*, the act of focusing on one particular aspect of visual information, while simultaneously ignoring those aspects not of interest (Broadbent, 1958; Desimone & Duncan, 1995).

Attention can be a *top-down* process, where focus is consciously and purposely orientated toward an item (Connor et al., 2004). This is usually goal directed and relating to a specific task. For example, finding a friend on a crowded train platform requires internally orienting one's attention to searching for a specific person. Alternatively, attention can be drawn, even unwillingly, towards a stimulus in a *bottom-up* fashion (Berger et al., 2005). Consider you are still searching for your friend but suddenly a pigeon flies towards your face. You will shift your focus to the bird and move reflexively out of its way (Skarratt et al., 2014). In this situation, the stimulus is controlling your attention rather than being purposefully directed towards it. Cues that capture attention in this way can be behaviourally relevant (Skarratt et al., 2014). An object moving towards you requires more immediate attention than the task of finding a friend, because it is likely that a behavioural response is necessary. However, *bottom-up* attention capture can also occur in the absence of behavioural relevance (Theeuwes, 1994). You may return to searching for your friend to find your attention is drawn to someone wearing a large, brightly coloured hat. Your friend does not wear hats, and the presence of the hat does not require a behavioural response. Attention capture in this instance is driven by a conspicuous and novel (Becker & Horstmann, 2011), but entirely irrelevant, stimulus.

While multiple cues, or tasks, may be of interest at one time, prioritising the most behaviourally relevant is necessary for efficient processing (Desimone & Duncan, 1995). Attempting to divide attention reduces task performance in mammals due to competition at a neuronal level; multiple objects compete for neuronal representation in the visual cortex

(Rhesus macaques, *Macaca mulatta*; Moran & Desimone, 1985; Chelazzi et al., 1998). In non-mammals there is behavioural evidence of divided attention reducing performance in birds (Blough, 1992) and fish (Milinski, 1984). Target detection in blue jays (*Cyanocitta cristata*) is impaired when searching for two, rather than one, phenotype of computerised moths (Dukas & Kamil, 2001). A simulated predator, which otherwise captures attention, fails to do so when blue jays and three-spined stickleback (*Gasterosteus aculeatus*) are engaged in a demanding foraging task (Milinski, 1984; Dukas & Kamil, 2000).

When faced with a larger, denser group hungry stickleback are apparently less able to divide attention between the task of attacking prey and maintaining vigilance (Milinski, 1984). This is evidence that the complexity of a foraging task, increased by a greater number of densely spaced prey, reduces predator detection performance (Milinski, 1984). Similarly, behavioural performance in humans varies with task complexity (Alvarez & Franconeri, 2007; Zelinsky & Neider, 2008). For humans tracking simulated sharks, performance drops as the number of sharks within the scene increases (Zelinsky & Neider, 2008). It is generally accepted that the human threshold for successfully monitoring moving objects simultaneously is around 4-5 items (multiple object tracking, or MOT; Pylyshyn & Storm, 1988; Doran & Hoffman, 2010). However, when items move more slowly, or are further from their neighbours, dividing attention between 6-8 targets is possible (Alvarez & Franconeri, 2007). When items are fast moving or there is little space between them, tracking ability is reduced to 1-2 items (Alvarez & Franconeri, 2007). The complexity of a task should inform predator behaviour (Clark & Dukas, 2003). For example, searching for cryptic prey is more challenging than searching for conspicuous prey, therefore attention should be focused on one prey type as rather than divided between all available prey types (Dukas & Ellner, 1993; Dukas, 2004).

1.1 The confusion effect

From the perspective of prey species, the limitations of predator visual systems can be exploited to reduce predation risk (Stevens et al., 2011; Hogan et al., 2016). An example of this is the *confusion effect* (Krakauer, 1995; Tosh et al., 2006b). Larger prey group size (Landeau & Terborgh, 1986), higher density (Milinski, 1990), similarity of group members (Landeau & Terborgh, 1986) and unpredictable, coordinated movement (Ioannou et al., 2012; Scott-Samuel et al., 2015) are features that elicit the *confusion effect* in visually hunting predators. The *confusion effect* can manifest behaviourally as a reduced attack-to-kill ratio (Landeau & Terborgh, 1986), increased spatial error of attacks (Ioannou et al., 2009), increased attack latency (Milinski, 1979) and refusal to attack more confusing groups (Milinski, 1977). Predator *confusion* is so called because predators appear overwhelmed, or confused, when faced with large, dense prey groups. There is evidence that other sensory systems face similar limitations, resulting in olfactory (Tosh & Brogan, 2015) and auditory (Goodale et al., 2019) *confusion effect*s. The visual *confusion effect* is thought to stem from *perceptual bottlenecking* leading to an overburdened visual system (Krakauer, 1995).

Predators demonstrate higher success at capturing prey when there are fewer individuals competing for attention within the visual field (Schradin, 2000; Ioannou et al., 2009). However, when attacking a perceptually confusing prey group there are strategies that help predators to overcome their own cognitive limitations. Group size and density enhance predation *confusion* (Scott-Samuel et al., 2015; Hogan et al., 2017b), therefore breaking up a group to isolate an individual, before carrying out an attack, can increase a predators attack success (Jenkins, 2000; Turesson & Brönmark, 2007). This strategy is essentially engineering a situation where there are fewer items competing for attention within the visual field. Spatially isolated prey are preferentially targeted by stickleback predators (Milinski, 1977) and are caught more quickly by humans (Ruxton et al., 2007). However, computerised targets took longer to catch when in proximity to a confusing group compared to when they were alone (Ruxton et al., 2007). This suggests that the *confusion effect* may not be entirely overcome by preferentially targeting stray prey individuals. Prey at the edge of a group are also at increased risk of predation (Hamilton, 1971; Ioannou et al., 2012). Rather than being driven by a response to the *confusion effect* this has been attributed to the greater chance of edge prey encountering a predator before their more centrally positioned group mates (Duffield & Ioannou, 2017). However, while the selection of edge prey may not be primarily driven by *confusion*, it is still possible that *confusion* is a contributory factor.

1.2 The oddity effect

Another strategy for predators targeting confusing groups of prey is to focus on a target that is visually distinct to the other group members, this is termed the *oddity effect* (Ohguchi, 1978; Landeau & Terborgh, 1986). Odd individuals are targeted more often than expected by chance in field (Almany & Webster, 2004; Almany et al., 2007) and in laboratory based studies (Milinski, 1977; Ohguchi, 1978; Penry-Williams et al., 2018). When a group has confusing features, preferential targeting of rare or odd group members increases attack success of largemouth bass (*Micropterus salmoides*) predating minnow spp. (silvery, *Hybognathus nuchalis*; bluntnose *Pimephales notatus*; fathead *P.promelas* and stonehead *Campostoma anomalum*, Landeau & Terborgh, 1986; Theodorakis, 1989). The mitigation of *confusion* through the selection of odd prey has been demonstrated empirically (Landeau & Terborgh, 1986) but the influence of confusing group features, e.g. numerical group size (Landeau & Terborgh, 1986; Ruxton et al., 2007), on the selection of odd prey has not. The close conceptual link between *confusion* and *oddity* suggests that features that elicit predator confusion should also drive selection of odd prey. Theoretical models predict that the selection of odd prey should increase with increasing group size (Krakauer, 1995). If this were the case then odd prey would not have the same level of antipredator protection within a group than their majority phenotype group mates.

The grouping choices of fish species indicate a preference for avoiding *oddity*. Western rainbow fish (*Melanotaenia australis*, Rodgers et al., 2010), mollies (*Poecilia latipinna*, McRobert & Bradener, 1998) and female fighting fish (*Betta splendens*, Blakeslee et al., 2009) choose to associate with groups of similar coloured conspecifics. Furthermore, when presented with a choice between a single matched individual and a large, unmatched group, rather than preferring the group female fighting fish show no preference (Blakeslee et al., 2009). When part of a group, the behaviour of prey individuals suggests an increase in perceived predation threat occurs when they are a minority phenotype. Large three-spine stickleback (Peuhkuri, 1997) and female bighorn sheep (*Ovis Canadensis*, Meldrum & Ruckstuhl, 2009) spend a reduced time foraging when they are odd. Stoplight parrotfish (*Sparisoma viride*) will choose to leave a mixed group in order to hide, rather than remain as a minority, when under threat of predation (Wolf, 1985).

The point at which a minority phenotype becomes subject to preferential targeting by a predator can be considered the threshold of *oddity*. It is at this point that a minority phenotype individual should leave an unmatched group, rather than remain as an odd member (as observed in Wolf, 1985). A threshold for *oddity* has been demonstrated for bass predating minnow (Landeau & Terborgh, 1986). Bass directed more attacks than expected by chance towards minority coloured minnow when there were 1 or 2, but not 3, present within a group of 8. However, within the same predator-prey system, bass preferentially target size-odd minnow at a representation of 5:25 (Theodorakis, 1989). This difference may be due to the different types of *oddity* being observed (colour vs size).

Stickleback preying on *Daphnia* are the most commonly used predator-prey system for examining predator selection of odd prey (Ohguchi, 1978; Rodgers et al., 2013; Rodgers et al., 2014; Penry-Williams et al., 2018; Raveh et al., 2019). However these studies (Rodgers et al., 2013; Rodgers et al., 2014; Penry-Williams et al., 2018; Raveh et al., 2019) consistently represent *oddity* as a single individual within a group, with the exception of (Ohguchi, 1978) where 2 odd individuals were present. Therefore, whether the threshold for colour *oddity* observed in bass-minnow interactions (Landeau & Terborgh, 1986) applies to other predator-prey systems has not been established.

1.3 Visual search and attentional capture

It is intuitive to think that odd prey capture attention due to their increased conspicuousness against the background of unmatched group mates and studies using target selection as a proxy for conspicuousness and attention capture do suggest this (Mokeichev et al., 2010; Ben-Tov et al., 2015). Attentional capture occurs before prey is selected, however there is no experimental paradigm for behaviourally demonstrating attentional capture prior to the attack stage of predation in non-human subjects. Experimental psychologists do have such paradigms in place for human subjects searching groups, or arrays, for preassigned targets in what are known as *visual search* tasks (Bundesen & Habekost, 2008). Tosh et al. (2009) highlighted this area of research as cognitive psychology’s equivalent to the study of the *confusion effect*. The breadth of experimental psychology studies addressing *visual search* problems has led to detailed knowledge in the area of human *visual search* and attentional capture (Egeth & Yantis, 1997; Turatto & Galfano, 2000; Skarratt et al., 2009; Skarratt et al., 2014). Tosh et al. (2009) suggest that knowledge amassed though the study of *visual search* could be used to inform future work on predator *confusion* and the *oddity effect*.

Visual search is a perceptual task, which requires the employment of *visual attention*. Most commonly, human studies use *reaction time* (*RT*) and/or *accuracy* to measure the efficiency of a participant finding a pre-assigned target amongst an array of irrelevant *distractors* (Moraglia, 1989; Bravo & Nakayama, 1992; Theeuwes, 1994; Hon et al., 2016). These studies will often manipulate *set size* (the number of items within the array) and use *RT* x *set size* plots (Figure 1.1) to compare line slopes in order to infer information about search mechanisms (Wolfe & Pashler, 1998). Steeper slopes, indicating a positive relationship between *RT* and *set size*, represent inefficient *serial search*. When the slope is near zero, indicating no difference in *RT* between *set size*s, efficient *parallel search* is represented. In *serial search* items are attended individually until the pre-determined *target* is located. When search is *parallel*, however, all items in the scene are attended at once, i.e. in *parallel* with each other.

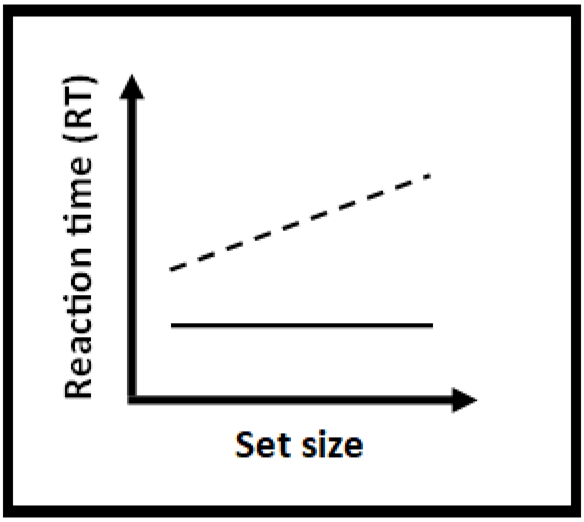

Figure 1.1 An example of a typical search efficiency plot used by cognitive psychologists. The dashed line, where a positive relationship between RT and set size is evident, indicates serial search. The unbroken line shows no change in RT as set size increases and therefore indicates parallel search.

Visual search studies examining search efficiency across *set size*s have, in the past, focused primarily on human (Bundesen & Habekost, 2008) and non-human primates (Dursteler & von der Heydt, 1992; von der Heydt & Dursteler, 1993; Bichot et al., 2001; Ogawa & Komatsu, 2004). More recently, this *visual search* paradigm has been extended to examine search efficiency in bees (honeybee Apis mellifera, Spaethe et al., 2006; bumble bee Bombus terrestris, Chittka & Spaethe, 2007; honeybee, Morawetz et al., 2014), zebrafish (*Danio rerio*, Proulx et al., 2014), archer fish (*Toxotes. jaculatrix*, Mokeichev et al., 2010; *T. chatareus*, Rischawy & Schuster, 2013; *T. chatareus*, Ben-Tov et al., 2018) and barn owls (*Tyto alba*, Orlowski et al., 2015). Experimental protocol is adapted to suit the behavioural ecology of each species, for example bees search for pre-assigned target 'flowers' amongst increasing numbers of *distractor* 'flowers' (Chittka & Spaethe, 2007) and archerfish shoot aerial LCD displays in the same way that they target their natural prey (Ben-Tov et al., 2015). The aforementioned studies all focus on the physical selection of targets with the exception of Orlowski et al. (2015). The characteristic searching behaviour of owls, i.e. the lack of eye movement independent of head movement, allows measurement of attentional allocation prior to physical selection of targets in a way that is not possible in studies using fish, for example.

The processes necessary for carrying out *visual search* and the allocation of attention occur in the neocortex of humans (Bundesen et al., 2005). Despite the absence of a neocortex, similar search abilities to humans have been demonstrated by owls (Orlowski et al., 2015), archerfish (Mokeichev et al., 2010; Rischawy & Schuster, 2013; Newport et al., 2016; Saban et al., 2017) and zebrafish (Proulx et al., 2014). Specifically, these species have all demonstrated that they are capable of *parallel search*, efficiently finding a visually distinct target independent of *distractor* number. Bees, however, take a greater time to find a coloured target as *distractor* number increases, a finding consistent with inefficient *serial search* taking place (Spaethe et al., 2006; Chittka & Spaethe, 2007).

The efficient *parallel search* demonstrated by owls (Orlowski et al., 2015) and archerfish (Ben-Tov et al., 2015) is consistent with the *pop-out*, or singleton, effect. The *pop-out effect* is where a distinct singleton within an array captures attention in a *bottom-up* manner, facilitating efficient search. Similarly to the *oddity effect*, *pop-out* occurs when there is a visually distinct singleton present within an aggregation. Figure 1.2 is an example of an array used in a *visual search* experiment that contains a luminance contrast singleton, which pops out from the surrounding *distractors*. When presented with the arrays seen in Figure 1.2 human subjects, and other species capable of *pop-out*, will be able to easily detect the singleton and reaction time will be unaffected by the number of *distractors* present (Rischawy & Schuster, 2013). Conversely, bees, for example, would be unable to use the visual distinctiveness of the odd singleton to facilitate efficient *parallel search* (Spaethe et al., 2006;

Chittka & Spaethe, 2007). If the array were made up of active and mobile prey items, based on the predictions of the *oddity effect* it would be expected that a visual predator would preferentially target the odd singleton (Theodorakis, 1989; Penry-Williams et al., 2018). However, unlike *pop-out* preferential targeting of odd prey may not be independent of group size. Neural network models suggest that odd prey may be increasingly targeted in larger prey groups (Krakauer, 1995). In smaller groups the *confusion effect* may not occur. Therefore prey may be targeted randomly or on the basis of different features besides visual distinctiveness, such as body size (Raveh et al., 2019) or proximity to the predator (Duffield & Ioannou, 2017).

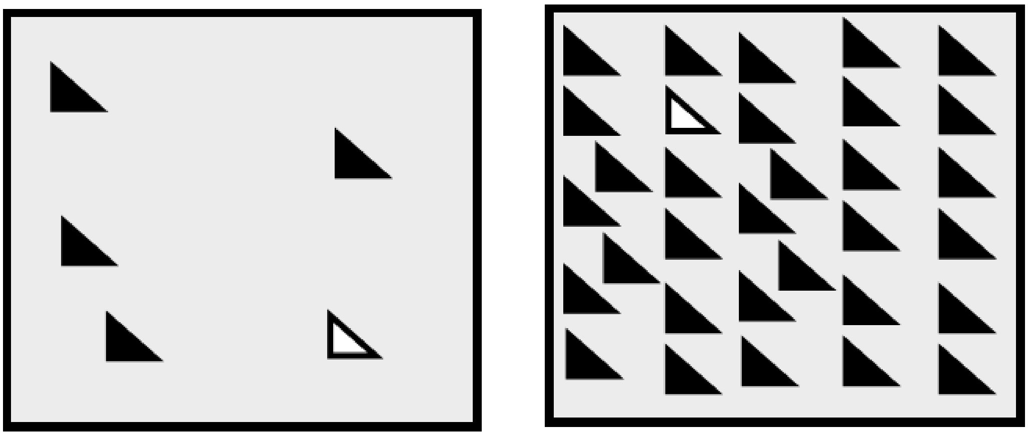

Figure 1.2 An example of the computerised stimuli arrays commonly used in visual search and attentional capture experiments.

1.4 Similarities between the confusion and oddity effects and principles from psychology

Oddity and *pop-out* make slightly different predictions and function at different stages of the predation cycle (attack vs. detection, Jeschke et al., 2002). However, there is obvious overlap between the findings of studies into behavioural ecology's *confusion* and *oddity effect*s and experimental psychology's work on *visual search*, as illustrated Table 1.1. Both *pop-out* and *oddity* appear to ease the challenge of *visual search* that is associated with detecting or attacking a target within a large aggregation. In the case of *pop-out*, the difficulty of searching an array containing many, similar looking items in order to detect a pre-determined target is eased when the target is visually distinct (Table 1.1, appearance). Therefore visual hunters are able to maintain detection speed. The *oddity effect* appears to ease the *confusion* associated with attacking larger groups of similar looking prey individuals (Landeau & Terborgh, 1986). This allows visual predators to maintain their rate of attack. Studies into *visual search* and the *confusion effect* have identified array, or group, features than slow detection time and attack rate, respectively (see Table 1.1, group structure). Similarly, studies investigating the *pop-out* and *oddity effect*s have demonstrated that focusing on odd targets can mitigate these effects at the detection (*pop-out*, Orlowski et al., 2015) and attack (*oddity effect,* Ruxton et al., 2007) stage of the predation cycle. Studies into the predatory response to *oddity* have focused exclusively on the attack, rather than detection stage of the predation cycle, and so the principles of *pop-out* could be used to examine how *oddity* may function at the stage prior to attacking a prey group. Predictions based on the *pop-out effect* would suggest that *oddity* would function at the earlier detection stage of the predation cycle, prior to an attack being carried out, possibly capturing attention and thus easing the challenge of confusing *visual search*. It is unknown if the detection of odd prey, prior to the attack stage of predation, interacts with group features previously identified as eliciting and enhancing predator *confusion*.

Table 1.1 Examples of areas of overlap between behavioural ecology and cognitive psychology in the study of visual search behaviour.

		Ecology findings	Psychology findings	Eco. species & ref.	Psy. ref.
Appearance	Homogeneity	Fish choose to shoal with similar looking individuals.	Finding a target takes less time the more homogenous the *distractors* are, and the more different the target is to the *distractors*.	(Western rainbow fish; Rodgers et al., 2010)	(Duncan & Humphreys, 1989)
		Presence of colour *oddity* increases the chance of any group member being caught.		(Largemouth bass preying on silvery minnows; Landeau & Terborgh, 1986)	
	Colour	Odd individuals are attacked more often than non-odd group members.	Colour singletons capture attention.	(Three-spine sticklebacks preying on *Daphnia*; Ohguchi, 1978)	(Turatto & Galfano, 2000)
	Size	Where no size is preferred, odd sized prey are targeted.	Large singletons capture attention.	(Largemouth bass preying on minnows; Theodorakis, 1989)	(Proulx & Egeth, 2008)
	Luminance	-	Luminance contrast singletons capture attention.	-	(Enns et al., 2001; Proulx & Egeth, 2008)

Table 1.1 continued		**Ecology findings**	**Psychology findings**	**Eco. species & ref.**	**Psy. ref.**
Behaviour	Movement	Fast moving prey are targeted over slow moving prey.	A moving target surrounded by still *distractors* is easier to find than a still target amongst moving *distractors*	(Thee-spine sticklebacks preying on dead Chironomid larvae; Ibrahim & Huntingford, 1989)	(Dick et al., 1987)
		Prey freeze in response to a perceived thread	Onset of motion captures attention	(Cod *Gadus morhua* responding to a mechano-acoustic "threat", Meager et al., 2011)	(Jonides & Yantis, 1990)
	Task urgency	Hungry fish are willing to feed on visually confusing groups, but become unaware of the presence of a predator. Sated fish maintain vigilance by choosing 'easy' prey.	Looming motion is prioritised because it is behaviourally most urgent. Looming motion primes the motor system for a faster response time.	(Thee-spine sticklebacks preying on *Daphnia*; Milinski, 1984)	(Skarratt et al., 2014)
	Divided attention		Humans are more likely to collide with obstacles when their attention is divided.		(Chen et al., 1996)

Table 1.1 continued.		**Ecology findings**	**Psychology findings**	**Eco. species & ref.**	**Psy. ref.**
Group structure	Group size/density	Attack latency increases with group size/density	*RT*s longer with larger/denser *set size*s (density effects), unless the target is a unique (odd).	(Bluegill sunfish predator preying on simulated prey; Ioannou et al., 2012)	(Cohen & Ivry, 1991)
		When (immobile) prey are presented at high densities, birds choose rare targets		(UK garden birds preying on pastry baits stuffed into Cepea hortensis shells; Allen & Weale, 2005)	
		Group density is less important in predator *confusion* than total group number (measured by predator preference).	Nearest neighbour distances (density effects) are less important than set-size in a *visual search* task.	(Thee-spine sticklebacks preying on Daphnia; Ioannou et al., 2008)	(Põder, 2002)
		Higher local density increased spatial error of attacks	Higher densities increase search times through.	(Three-spine sticklebacks preying on Daphnia; Ioannou et al., 2009)	(Wertheim et al., 2006)

The exact mechanisms that contribute to the amelioration of *confusion effect* by *oddity* are unknown. The parallels drawn by Tosh et al. (2009) between concepts of *visual search* to their ecological counterparts suggest that, like *pop-out*, the effect of *oddity* is a consequence of attentional capture. Ecologically speaking, the point at which a minority phenotype within a group begins to automatically attract attention would have consequences for minority type, odd, individuals and possibly the group as a whole (Rodgers et al., 2013; Quattrini et al., 2018). Similarly to the preferential targeting of odd prey at the attack stage of predation, it would be expected that at a point below 50% representation within a group, the minority phenotype would be detected more easily than their majority type groupmates.

1.5 Saliency and attentional allocation

Pop-out eases the challenge of search because attention is automatically guided (Itti et al., 1998). The automatic nature of *bottom-up* attentional capture results from features within the visual scene being processed before the conscious mind is engaged in this task. This is known as *pre-attentive* processing (Öhman, 1997; Wolfe & Pashler, 1998). Feature integration theory (Treisman & Gelade, 1980; Wolfe & Pashler, 1998) and the guided search model (Wolfe, 1994) state that simple features of objects, such as colour and orientation, are processed *pre-attentive*ly, i.e. without conscious engagement. The guided search model (Wolfe, 1994) goes on to state that *pre-attentive* information forms a type of 'map'. This map is used to inform which areas, or items, within a scene should receive attentional priority. The idea of a 'map' for attentional deployment has been expanded upon into the *Saliency map* model (Itti et al., 1998; Itti & Koch, 2000). Areas of contrast are identified as being *salient*, i.e. worthy of note, and the most *salient* region is attended to in a *bottom-up* fashion (Itti

& Koch, 2001). In the example used towards the beginning of this section, our attention was diverted away from the task of finding our friend and drawn towards a large, colourful hat. The size and vibrancy of the headwear strongly contrasted against the crowd of commuters present on the dull, grey train platform. As a result the hat was the most *salient* area of the scene and therefore captured attention. If the area of highest contrast within a scene is the target, e.g. our friend, search is efficient, as is the case for *parallel search*. If it is not, then items are attended to in *serial* (Treisman & Gelade, 1980), e.g. people are scanned one by one until the target person is spotted.

The theoretical underpinning of *saliency mapping* has been applied to animal behaviour (Pike, 2018; Bian et al., 2019; Kane et al., 2019). The time taken by quails (*Coturnix japonica*) to detect and attack cryptic artificial moths is predicted by prey *salience* (Pike, 2018). The eyespots on peacock (*Pavo cristatus*) tail feathers are associated with female mate choice (Dakin & Montgomerie, 2011), and *saliency mapping* highlights these as areas of high contrast in peafowl vision (Figure 1.3). Lower eyespot contrast is observed when similar images are modelled in the vision of an unintended audience, namely a dichromat mammalian predator (Kane et al., 2019). In the absence of computed *saliency map*s, target choice has been attributed to the *salience* of targets in archerfish (Mokeichev et al., 2010; Rischawy & Schuster, 2013; Ben-Tov et al., 2015) and this has been found to have a neuronal basis (Ben-Tov et al., 2015). Ben-Tov et al. (2015) identified a group of neurons that increased firing rate in response to the presence of odd items, i.e. those that contrasted against *distractors*. The positive association between the *salience* of an object and the firing rate of the associated neurons has been demonstrated in mammals (Smith et al., 2000) but this was the first evidence in a non-mammalian species.

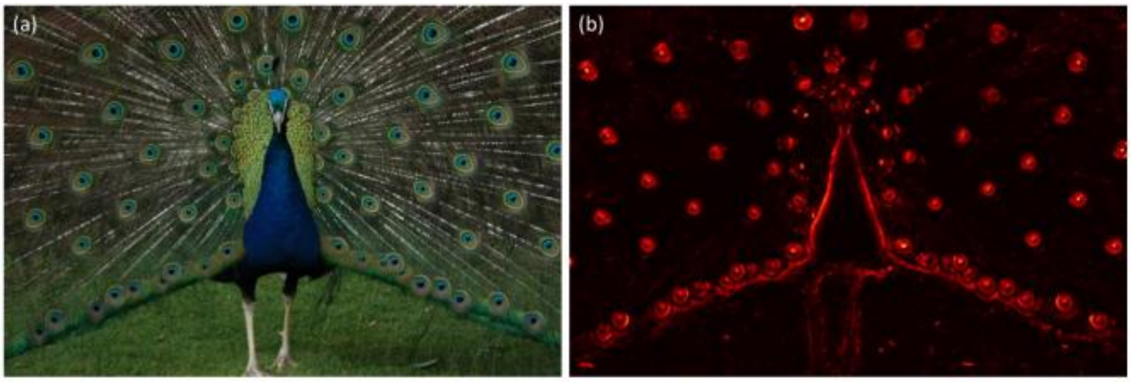

Figure 1.3 Adapted figure from (Pike (Pike, 2018), 2018) showing a) an image of displaying peacock and b) the areas of colour contrast, which highlight the salience of eyespots. Mapping by (Pike, 2018) was generated using data on peafowl's photoreceptor spectral sensitivity obtained from (Hart, 2002). See Box 1 – 'saliency' for unabridged figure. Image licensed under Creative Commons Attribution-Non Commercial 4.0 International: http://eprints.lincoln.ac.uk/31915/

The identification of a neuronal basis to *saliency map* formation in archerfish (Ben-Tov et al., 2015) is an example of discovery based on principles once thought to be uniquely relevant to humans and other mammals. There is a large base of research, in the area of experimental and cognitive psychology, which can be drawn upon to inform and advance research on predator-prey interactions (Table 1.1). Table 1.1 is not exhaustive, but highlights some of the research specifically relating to predator *confusion* and prey *oddity*. In addition to using principles from experimental psychology to inform research (Tosh et al., 2009), methodology can also be adapted and applied to suit ecological questions (Mokeichev et al., 2010; Orlowski et al., 2015). Experimental psychology tends towards the use of computerised arrays, presented to human subjects (Bundesen, 1990). The high degree of control that computerised arrays allow appears ideal for studying the *oddity effect*, and computerised stimuli have been demonstrated as appropriate for studying *pop-out* in non-humans (Ben-Tov et al., 2015). Computerised stimuli have been used to observe human predating odd targets (Ruxton et al., 2007), however their validity for studying the *oddity effect* in non-humans is yet to be established.

1.6 Aims and objectives

The objectives of this project are to firstly validate the use of computerised stimuli for studying the *oddity effect*. Once established, this method can be used to explore how *oddity* interacts with group features (e.g. numerical group size) and group composition (e.g. the number of odd prey within a group). In addition, the same methodology can be adapted to use human predators to look at *oddity* and attention capture, examining how *oddity* may function prior at the detection stage of the predation cycle.

The key research questions in this thesis aim to address the following:

1. Can experimental psychology be used to inform an improved methodology for studying the *oddity effect*? (Chapter 2)
2. At what point within a mixed group does an odd phenotype become subject to preferential targeting? (Chapter 2)
3. Are odd prey preferentially targeted more often in more 'confusing' groups? (Chapter 3)
4. How does the presence of *oddity* affect the difficulty or ease of *visual search*? (Chapter 4)
5. At what point within a mixed group does an odd phenotype capture attention? (Chapter 5)

Aims 1-3 focus on the choice of prey by stickleback predators. Aims 2-3 are concerned with under what conditions the *oddity effect*, as defined by preferential targeting of odd prey, occurs. Finally, aims 4-5 focus on *oddity* and attentional capture, using human predators.

Chapters 2-3 use stickleback predators preying on psychology inspired computerised arrays, or ‘prey-dot’ groups. Chapters 4-5 use human predators searching prey-dot groups for a predefined target. In chapters 2-4 concepts from psychology are discussed alongside those from behavioural ecology in order to holistically interpret the findings therein.

1.7 Box 1. Key terminology listed alphabetically. Key terms are *italicised* in text.

Accuracy

Accuracy may refer to the binary correct/incorrect (Ruxton et al., 2007) or spatial measure of the precision of *target* selection (Ioannou et al., 2009).

In psychological literature binary *accuracy* is typically represented as proportional data representing the number of correct responses made in a *visual search* task. For example, a participant may be asked to report whether or not a target is present within an array. The proportion of correct responses would be reported along with *RT* (Wolfe, 1994).

Within this thesis the measure of *accuracy* is made explicitly or contextually clear. For human subjects, within both the experiments presented and the cited literature, *accuracy* refers to a binary outcome. For non-human subjects *accuracy* is a spatial measure unless stated otherwise.

Bottom-up attention

See *visual attention*

Confusion effect – confusing group features

The *confusion effect* is an antipredator benefit that arises from prey group formation (Krause & Ruxton, 2002). Group features shown to elicit and enhance visual predator *confusion* are the a greater number of individuals within a group (Hogan et al., 2017b); the higher density of a group (Scott-Samuel et al., 2015), particularly *local density* (Ioannou et al., 2009); the similarity of group members (Landeau & Terborgh, 1986) and agile (Jeschke & Tollrian, 2007) and unpredictable movement (Scott-Samuel et al., 2015). Note the similarities between *confusing* group features and those that increase the challenge of *visual search* (Table 1.1) and *multiple object tracking* (see also *multiple object tracking MOT*).

Groups that have *confusing* features elicit a reduction in attack success (Landeau & Terborgh, 1986; Schradin, 2000). This is demonstrated behaviourally through an increased reluctance to attack confusing groups (Milinski, 1977), increased attack latency (Schradin, 2000), a reduced attack-to-kill ratio (Landeau & Terborgh, 1986) and increased spatial error of attacks (Ioannou et al., 2009)

The *confusion effect* is thought to arise from cognitive limitations, relating to processing capacity, such as *perceptual bottlenecking* (Krakauer, 1995)– see *perceptual bottleneck*. The *confusion effect* most commonly refers to visual *confusion*, however there is evidence that the tactile (Jeschke & Tollrian, 2007), olfactory (Tosh & Brogan, 2015) and auditory (Goodale et al., 2019) systems of predators face similar limitations.

Distractors – *foil, set size*

In *visual search* studies pre-determined *target* items are presented amongst varying numbers of irrelevant, usually uniform items, known as *distractors* (e.g. Feria, 2012). The number of items within a *visual search* scene, or array, is referred to as *set size* (e.g. Põder, 2002). *Set size* is manipulated through the number of *distractors* present. The purpose of *distractors* is typically to ascertain whether they do, in fact, distract from the task of finding a pre-determined *target* (Bruce et al., 2003). In the absence of *salient target* that captures *visual attention* increasing the number of *distractors* (and therefore *set size*) will increase *RT*, indicating more challenging search. In the presence of a *salient target* that captures *visual attention distractor* number should be unimportant (Wolfe, 1994).

Distractors are also referred to interchangeably as *foils* (Colman, 2015).In this thesis, when a *distractor* is the *salient items* that is intended to capture *visual attention* it is referred to as a *foil*.

Dot type

See also – *group type*

Within Chapters 4 and 5 of this thesis, *dot type* is used to categorise prey-dots on the basis of whether the target square is present or absent, and which (if any) prey-dot is odd. The first two letters define the presence or absence of the target (T): P = Present, A = Absent. The second two letters define the identity of the odd dot (O): T = Target odd, F = Foil odd, N = No *oddity*.

Feature contrast, feature singleton

See also – *pop-out*

Features that guide *bottom-up attention capture* are usually rare or unique within a scene and differ on a single feature, e.g. colour (Wolfe & Horowitz, 2017). If only a single item has this particular feature dimension, e.g. a single red circle within many green circles, that item can be referred to as a feature singleton (Wolfe, 1994). The *feature contrast*s against the features of the other items within the array (Nothdurft, 2000). *Feature contrast* has been shown to guide attention on the attributes of colour, motion, orientation and size (Wolfe & Horowitz, 2017). Feature singletons *pop-out* from a visual scene.

Foil

See *distractors*

Group type

See also - *dot type*

Within Chapters 4 and 5 of this thesis, *group type* is used to categorise prey-dot groups on the basis of their numerical group size (4 or 16) and the area that they occupy (small area or large area). There are four possible *group type*s: 4-SA, 4-LA, 16-SA and 16-LA. The number defines the numerical group size and is followed by SA for small area, or LA for large area.

Multiple object tracking (MOT)

Within this thesis *multiple object tracking* (*MOT*) refers to the human ability to keep track of moving items within a scene (Sears & Pylyshyn, 2000; Vul et al., 2009). In psychology, *MOT* experiments are dynamic arrays containing multiple moving items. The arrays contain pre-defined *targets* and *distractor* items (Feria, 2012). Typically, all these items are identical with the pre-determined *targets* being identified prior to the onset of motion (Vul et al., 2009). When the items within the array begin to move the participant is required to keep track of the targets. After the array has ceased to move the participant is required to identify the *target* items to ascertain whether they were successful in tracking them (Vul et al., 2009).The performance of participants is used to investigate cognitive processing and attentional capabilities (Sears & Pylyshyn, 2000; Doran & Hoffman, 2010). Performance is reduced by similar “group” features as those that enhance predator *confusion* (See *the confusion effect*) and limit human *visual search*: the number of items, the density of items, the similarity of the items and the speed at which they move (Vul et al., 2009; Feria, 2012).

Oddity effect

See also – *the confusion effect*

The *oddity effect* is where prey that are conspicuously distinct to their group-mates are preferentially targeted (Ohguchi, 1978).

The *oddity effect* ameliorates the *confusion effect* through increased attack success when odd prey are targeted, or simply present, within a group of otherwise similar looking individuals (Landeau & Terborgh, 1986). In addition to the selection of prey by predators, the *oddity effect* is evident through the grouping behaviours of prey species (Croft et al., 2009). *Oddity* will be avoided through assortative grouping (Rodgers et al., 2010), and odd individuals within a group will demonstrate behaviours associated with increased perception of predation risk, such as decreased foraging activity (Peuhkuri, 1997).

A conspicuous difference to group-mates is an important factor, as odd individuals are not targeted if they are cryptic within a group with a non-cryptic majority (Rodgers et al., 2013). The *oddity effect* is also absent where asymmetry of risk is present (Mathis & Chivers, 2003). For example, single armoured brook sticklebacks (*Culaea inconstans*) prefer to associate with a more vulnerable species (fathead minnow, *Pimephales promelas*) under higher predation risk.

Parallel search

Cognitive psychologists propose that, when searching a scene, the visual processing of the items within that scene can occur in two ways: serially (*serial search*) or in *parallel* (Treisman & Gelade, 1980). For easy, efficient searches the items within the scene are said to be inspected all at once, or in *parallel* to one another (Treisman & Gelade, 1980).

Parallel search is identified by comparing the *reaction time (RT)* data of different *set sizes*. If there is no statistical difference in *RT* for numerically small and large *set sizes*, then this indicates *parallel processing* of the items within the scene (e.g. McElree & Carrasco, 1999). *Parallel search* is evident for the *pop-out effect* (Treisman & Gelade, 1980).

Perceptual bottleneck

Perceptual bottlenecking occurs in the context of information processing within sensory systems (Swanson, 1977; Tombu et al., 2011). It is a metaphorical term coined to illustrate the limitations of sensory processing, i.e. that the flow of information is restricted as it travels through a sensory system. Bottlenecking results from more information being available to a perceptual system than can be processed, and therefore perceived, efficiently at one time (Bingham, 1988). A consequence of *perceptual bottlenecking* is that some information must be ignored in order for other information to be attended to (see *visual attention*) and processed (Swanson, 1977). The principle of *perceptual bottlenecking* therefore underpins the concept of selective attention, where important information is attended to over irrelevant noise – see *signal-to-noise ratio* (Swanson, 1977).

Pop-out effect – singleton

See also - feature *contrast*

The *pop-out effect* occurs when an individual item (a *singleton*) within a scene contrasts with its surroundings sufficiently enough to stand out and capture attention (Ben-Tov et al., 2015; Orlowski et al., 2015). Items that *pop-out* do so due to *feature contrast* (Nothdurft, 2000).

The criteria for identifying *pop-out effect* is no increase in *RT* between *set size*s, *pop-out* searches are processed in *parallel* (Wolfe, 2016).

Pre-attentive

Pre-attentive processing is the first stage of visual processing, occurring before conscious *visual attention* takes place (Treisman & Gelade, 1980; Wolfe, 2016). *Pre-attentive* processing occurs in the case of efficient *parallel search* and *pop-out*.

RT - reaction time, response time, response latency

Frequently in experimental psychology participants are instructed to make a specific response to a stimulus or multiple stimuli. The time take from the presentation of the stimulus to the participant's response is called *reaction time (RT)* and is measured in milliseconds or seconds. In *visual search* experiments the 'specific response' participants are instructed to make often involves pressing a button, or key of a computer keyboard, once they locate a target item. This is the case in Chapters 4 and 5 of this thesis.

Comparisons of *RT***,** between treatments within an experiment, are used to make inferences about the speed at which information is processed, and therefore, the difficulty of a task (Wolfe, 1994). A more difficult task will take longer to process and *RTs* will be greater than for an easier task. *RT* can also be used to indicate attentional allocation and capture. For example, a participant can be instructed to find a *target* stimulus and report when they have located it. In some trials the *target* stimulus is presented alone, in others irrelevant stimuli (see *distractors*) are presented alongside it. The *RTs* of these two conditions can be compared, if *RTs* are longer when the irrelevant stimuli are present this is evidence that it has captured attention. If there is no statistical difference between the RTs of the two treatments then the participant's attention was not shifted away from the task.

Saliency – *salience*, *saliency map*s

Saliency within this thesis refers to visual *salience*, unless otherwise stated.

Saliency refers to the prominence or conspicuousness of an object in comparison to its surroundings (Pike, 2018). In *visual search* a *target* increases in *salience* the more dissimilar it is to the surrounding *distractors* (Wolfe & Horowitz, 2017).

How *salient* an object is can be quantified by increased neuronal firing in brain regions associated with the stimulus (Reynolds & Desimone, 2003), behavioural responses that indicate attention capture by the stimulus (Fecteau & Munoz, 2006) or though the formation of *saliency maps* (Itti et al., 1998).

Saliency maps are computed, neurologically (Li, 2002) or through digital image analysis (Pike, 2018) to highlight which regions of a scene or image are most *salient*, i.e. those which should be attended to. Cortical *saliency maps* are theorised to explain which visual information is prioritised within the brain (Koch & Ullman, 1987; Itti et al., 1998). It is proposed that multiple sub-maps are formed at different stages of visual processing, before combining to create a master *saliency map* (Koch & Ullman, 1987; Itti et al., 1998). Each region within the scene is ranked on the basis of their contrast to their surroundings. This occurs for each individual feature, e.g. colour, orientation and luminance, generating multiple 'feature maps' for each item. These separate feature maps are combined into ‘conspicuity maps’, where each item is ranked on the basis of contrast for their combined features (Koch & Ullman, 1987; Itti et al., 1998). Finally, all the maps are combined to give a final *saliency map* that highlights the areas of greatest contrast within a scene. This overall *saliency map* is considered a priority map for attentional deployment (Zhaoping, 2016). The formation of sub-maps is disputed and it is possible that *saliency map*s are computed without the prior individual features maps, within the V1 region of the brain (Li, 2002). Dispute over neurological processes aside, the outcome is agreed upon: the most salient region within the scene captures attention (Fecteau & Munoz, 2006).

Digital *saliency map* models rank each pixel within an image based on its contrast for different features, similarly to the theoretical ‘feature maps’, the ranks of the pixels are combined and weighted to give a final overall *saliency map* (Zhai & Shah, 2006; Pike, 2018). For a digitally computed *saliency map* the final image output is usually greyscale or dichromatic, with areas of brightness indicating the most *salient* regions. For example, for a greyscale image the areas of white would indicate the most *salient* regions. In Figure 1.4 (overleaf) the areas of bright red indicate the regions of highest contrast.

Figure overleaf.

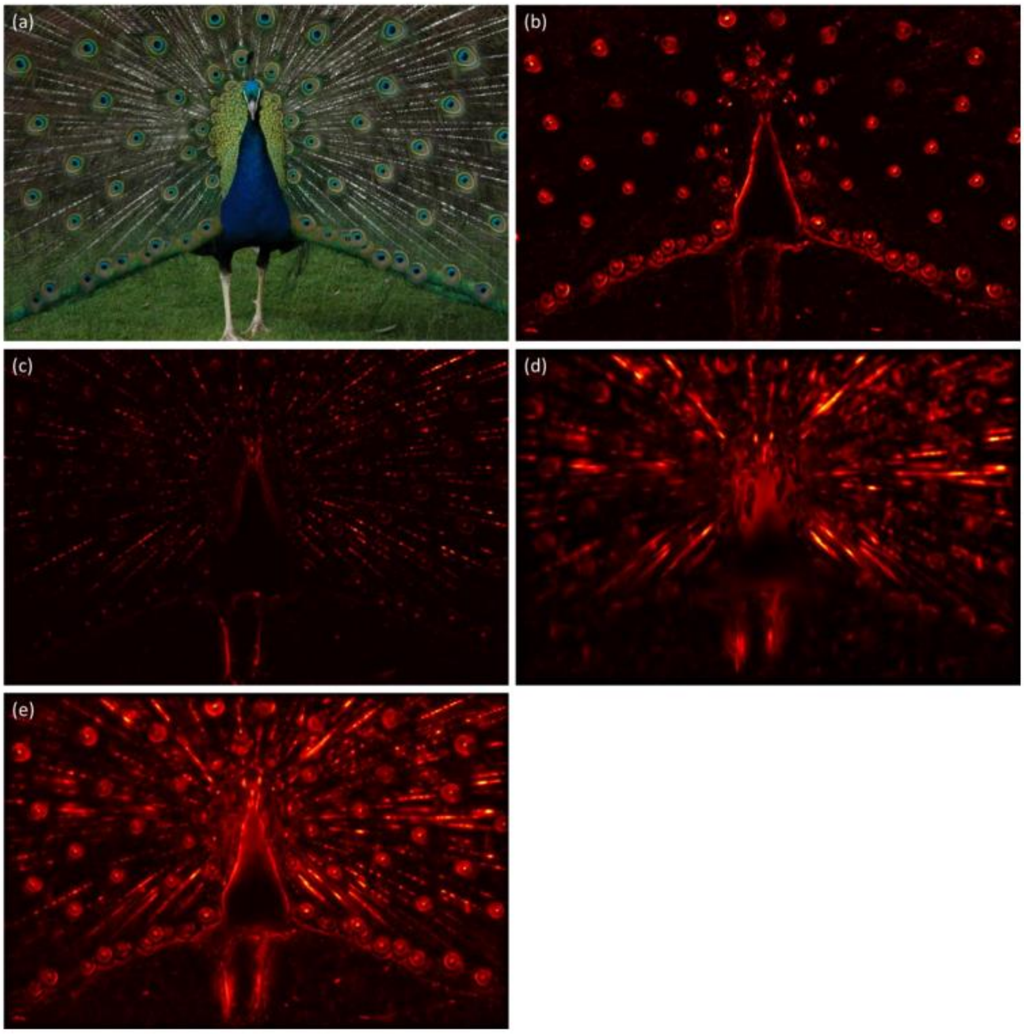

Figure 1.4 Figure and caption from (Pike, 2018): "(a) Calibrated colour image of a displaying peacock (Pavo cristatus), and the conspicuity maps for (b) colour, (c) luminance and (d) orientation that result from applying the model of visual salience used in this paper. (e) The final overall saliency map. In each map, colour is proportional to salience, with lighter colours denoting regions of relatively high salience and darker colours regions of relatively low salience. The procedure used was as described for experiment 2, but using data on the peafowl's photoreceptor spectral sensitivity from Hart (2002)." Image licensed under Creative Commons Attribution-NonCommercial 4.0 International: http://eprints.lincoln.ac.uk/31915/

Serial search

see also *parallel search*

The converse of *parallel search* is *serial search*. When visually processing a scene, the items within the scene are inspected individually, or in *serial*.

RT for *serial search* increases with *set size*, the greater number of *distractors* present means that a greater number of items need to attended in order to find the *target*.

Set size

See *distractors*

Signal-to-noise ratio – *visual noise*

This term originated as a measure of electrical signals however, the usage within this thesis refers to the commonly used, metaphorical description of useful vs. irrelevant visual information.

For example, Jacky dragons (*Amphibolurus muricatus*) wave their limbs to communicate with conspecifics. This communicative signal is received less effectively when the plants surrounding the animal are being moved by the wind (Bian et al., 2019). The signal of waving must compete with this surrounding visual 'noise' of the plant movement (Bian et al., 2019).

Target

When used as a noun, *target* can refer to the subject of an attack made by free choice (e.g. Rodgers et al., 2013; Penry-Williams et al., 2018) or a pre-determined item that subjects are trained (Ben-Tov et al., 2015; Orlowski et al., 2015) or instructed (Hogan et al., 2016) to detect (Bravo & Farid, 2004) or 'attack' (Ruxton et al., 2007). Within this thesis the distinction should be contextually clear, for stickleback participants *target* refers to the former, while for human participants *targets* are pre-assigned.

Top-down attention

See *visual attention*

Visual attention

For the purpose of this thesis, *visual attention* refers to the fixation or selection of visual cues within the environment (Bruce et al., 2003). Visual attention may be guided by internal goals (*top-down*), captured by the features of a stimulus (*bottom-*

up) (Connor et al., 2004) and may be focused on one task, or divided between tasks (Dukas & Ellner, 1993).

Visual attention can be represented neuronally, by the increased firing rate of neurons within brain regions associated with the stimulus (Reynolds & Desimone, 2003). The focus of *visual attention* can also be identified through behavioural measures such as *reaction time* (see *reaction time RT*), or task performance (Milinski, 1984; Dukas, 2002b).

Visual search

Visual search refers to the perceptual task of finding an item, or items, within a scene. Visual search is an essential real world task for all visually driven animals, for example Figure 1.2 shows *visual search* behaviour in the contexts of foraging and vigilance.

In the field of psychology *visual search* experiments typically measure the time taken (*RT*) to find a pre-defined *target*. Thus allowing inferences to be made about *visual attention* and search efficiency (see also - *parallel search* and *serial search*). *Set sizes* vary and *targets* may differ from *distractors* on a single feature, e.g. colour, or on multiple features, e.g. colour and orientation (Bundesen & Habekost, 2008). Performance in *visual search* is reduced by the number of items within an array (Wolfe, 1994), the similarity of items (Duncan & Humphreys, 1989) and crowding of these items (Levi, 2008) – note the similarity between the features that reduce *visual search* performance and those that limit *multiple object tracking* and enhance *the* predator *confusion effect*. The efficiency of *visual search* is enhanced by *feature contrast,* see also – *pop-out effect* and *the oddity effect.*

Figure 1.5 Left, a foraging chicken (Gallus gallus domesticus) searches through the undergrowth and right, a vigilant meerkat (Suricata suricatta) watches for predators while on sentinel duty.

Both images are licensed are under the Creative Commons Attribution-Share Alike 2.0 Generic license. Left photo credit: Artelnjeru, https://commons.wikimedia.org/wiki/File:Chicken_pecks.jpg. Right photo credit: Cotswold Wildlife Park, https://commons.wikimedia.org/wiki/File:Meercat_-_Cotswold_Wildlife_Park_(28959210220).jpg).

Chapter 2. Computerised stimuli for studying *oddity effect*s

2.1 Abstract

Visually hunting predators must overcome the challenges that prey groups present. One such challenge is the *confusion effect* where an overburdened visual system means predators are unable to successfully target prey. A strategy to overcome *confusion* is the targeting of distinct, or odd, individuals (the *oddity effect*). In live prey experiments, manipulation of group member phenotypes can be challenging and prey may differ on more than the single feature one intends to define as odd. The use of highly controllable computerised stimuli to study predator-prey interactions is increasingly popular in the field of behavioural ecology. However, to our knowledge, the validity of computerised stimuli to study the *oddity effect* has not been established.

Predator choice experiments were conducted using naive stickleback predators to ascertain whether the *oddity effect* could be demonstrated in the absence of live prey.

We found evidence for both the *oddity effect* and preferential targeting of group edges and low density regions, as would be predicted if predators targeted prey individuals to minimize *confusion*. The *oddity effect* was evident at a low threshold, above which dots were no longer perceived as odd, and no longer attacked more often than expected by chance.

We conclude that computerised stimuli are an improved, practical method for studying *oddity effect*s while further validating the use of similar methods for studying other aspects of visual predation. In addition to higher control of 'prey' appearance, the replacement of live prey animals with digital stimuli is ethically beneficial and reusing code improves experimental efficiency.

2.2 Introduction

When predators approach a group of prey they are simultaneously presented with a choice of potential targets. Which prey within a group are selected by predators directly affects the composition of phenotypes within a group, in addition to driving the evolution of prey grouping behaviours (Croft et al., 2009; Rodgers et al., 2014). Visually hunting predators may select prey because of their position in the group (Hamilton, 1971), or because of their appearance (Ohguchi, 1978). Prey may be preferentially targeted because they appear slow or weak (Genovart et al., 2010), because they are the appropriate size to maximize energy gains (Turner, 1982), or because they are visually distinct from the rest of their group (the *oddity effect*, see Box 1 for italicised key terms; Almany et al., 2007; Penry-Williams et al., 2018).

Landeau and Terborgh (1986) used bass preying on groups of minnow to demonstrate that the presence of visually distinct ‘odd’ prey mitigates the *confusion effect*. The *confusion effect* describes the diminished ability of a predator to successfully target an individual within a group, resulting from cognitive limitations (Krakauer, 1995). Landeau and Terborgh (1986) is a well-cited *oddity effect* study, showing how individual appearance and overall group composition can affect predation decisions and outcome. However, a methodology that uses live, vertebrate prey, which are confined with the purpose of being attacked, is something we are less likely to deem ethically acceptable by today’s standards (Buchanan et al., 2012; Brown, 2015; Sloman et al., 2019). A more common predator-prey system for studying *confusion* and *oddity effect*s is that of stickleback (*Gasterosteus aculeatus*) preying on *Daphnia*. Putting aside any philosophical questions about ethics and (the lack of) vertebrae (although see

Freelance, 2018), there are potential issues relating to efficiency and perception that may arise here.

In order to understand how phenotype contributes to the *oddity effect*, prey group members should ideally only differ by a single feature. Many studies examining predator selection of odd prey require prey individuals to be sorted by size and dyed, usually with food colouring (Landeau and Terborgh, 1986; Wilson et al., 1990; Richards et al., 2011; Rodgers et al., 2013; Penry-Williams et al., 2018). This process is time consuming and largely reliant on a human judgment of prey similarity. Perception is highly subjective, even between members of the same species (Brainard and Hurlbert, 2015) and consequently this raises potential issues for repeatability. In addition, studies of *confusion* and *oddity effect*s use the human visual system to establish uniformity of prey appearance, yet stickleback, for example, are able to see ultraviolet (UV) light (Modarressie and Bakker, 2007; Rick et al., 2012). Hence, what might appear to be a largely homogenous stimulus group in visible light might not be the case elsewhere in the electromagnetic spectrum. Although there are ways to overcome between-species perceptual differences (e.g., Rowe et al, 2006), we submit below that rendering digital stimuli monochromatically and through a UV-filter affords the highest standard of stimulus control.

An alternative to altering prey appearance is to use colour-morphs of the same species. In the case of *Daphnia*, morphs can be obtained through manipulating water chemistry (Ohguchi, 1978). However, different behavioural phenotypes often present themselves alongside differences in appearance. For example, higher levels of aggression are seen in melanic vs. silver mosquito fish (*Gambusia holbrooki*, Horth, 2003) and blue vs. yellow cichlids (*Astatotilapia burtoni*, Dijkstra et al., 2017). Black springbok (*Antidorcas marsupialis*) have lower activity levels than their white or standard coloured counterparts (Hetem et al., 2009), and while both black and white mollies (*Poecilia latipinna*) shoal with colour-matched conspecifics, white morphs have a stronger overall shoaling tendency (Rodgers et al. 2013). Uncontrolled differences in behavioural phenotype have the potential to confound studies that are aiming to isolate a feature that may influence predator choice.

As we suggest above, a possible solution to improve experimental efficiency and to better control prey phenotype is to use computerised stimuli in place of live prey. Individuals within simulated 'prey' groups can be manipulated to differ from their group-mates only in the specific, measurable ways intended by the experimenter. The use of computerised stimuli to study *visual search* and attentional capture is well established in experimental psychology (Bundesen and Habekost, 2008). There is also considerable research in the field of behavioural ecology examining the *confusion effect*, with human predators preying on computerised targets (Ruxton et al., 2007; Scott-Samuel et al., 2015; Hogan et al., 2017a; Hogan et al., 2017b). Computerised stimuli are also gaining popularity for studying some aspects of visual predation in non-humans (Ioannou et al., 2012; Woo et al., 2016; Duffield and Ioannou, 2017; Ioannou et al., 2019). However, to our knowledge, the effectiveness of similar methods for studying *oddity* is yet to be validated for non-human predators.

Here, we use stickleback targeting computerised prey-dots to establish the value of this approach to the study of the *oddity effect*, defined here as the preferential targeting of a minority phenotype (Ohguchi, 1978; Penry-Williams et al., 2018; Raveh et al., 2019). If the use of digital stimuli is a valid methodology for exploring *oddity effect*s, we would expect to see that a minority phenotype becomes preferentially targeted below a certain threshold of representation within the group. For applicability to the general study of visual predation, predators should target computerised prey groups as they do live prey groups. Thus, we would expect, in line with work on live prey, to also see preferential predation of those on the edges of groups (Hirsch and Morrell, 2011).

2.3 Methods

2.3.1 Stickleback sourcing and maintenance

Three-spined stickleback (n=56) were sourced from Thwaite Hall Gardens, Cottingham, UK (grid reference: TA 055 326) in October, 2015. A further 200, wild caught stickleback were sourced from The Carp Co. (Bourne Valley Fish Farm, Kent, UK) in September, 2016. Fish from the Thwaite Hall Gardens source were caught using telescopic landing nets and transported back to the laboratory, by car, in a 20L bucket filled with pond water. No fish died in transit or immediately after being transferred to the laboratory tanks.

All fish were quarantined for 3 weeks in two 150L tanks, aerated with two Tetra APS 50 air pumps and two 30 mm air stones per tank. Manual water changes of 25-50% were made 2-3 times per week. After this period, fish were housed in groups of 12 on a closed, freshwater system with ~20% new water introduced per week. Fish were fed daily on defrosted frozen bloodworms and *Daphnia* spp. (Ings Lane Garden Centre, Hull, UK). Water temperature was kept between 10-12°C and the day:night light cycle was set at 12:12 h to prevent the onset of breeding condition. As a result, no attempt was made to determine the sex of individual fish. Experimentation took place between 09:00 and 18:30 h, as stickleback are diurnal, visual predators (Wootton, 1976; FitzGerald and Wootton, 1986).

2.3.2 Experimental tank setup

Experiments took place in a modified glass aquarium (Figure 2.1). The aquarium was split into a companion area spanning the full width of the tank at one end (10 cm x 20 cm, Figure 2.1 a) and a larger focal area (20 cm x 20 cm, Figure 2.1 b). The companion area contained 3 non-experimental fish. The companion fish acted to reduce stress to the test fish by providing a social environment for this shoaling species (Jones and Godin, 2009; Voellmy et al., 2014). A transparent, perforated partition allowed visual and olfactory contact between the companion fish (in the companion area) and the focal fish (in the focal area). The walls of the companion area were covered with black, opaque plastic to minimize brightness, and therefore stress (Maximino et al., 2010), to the companion fish. An opaque lid covered the companion area so companion fish were not disturbed when focal fish were netted in and out of the experimental tank. The focal area of the tank was partially divided by a black, opaque barrier. This provided a shaded refuge area for the test fish, from which the projection (see below) was not visible. A plastic plant within the experimental area provided further refuge for the test fish.

Simulated prey (see below for details of the simulation) were rear-projected onto a self-adhesive, rear projection film (model: GR/Gray, brand: ARCHISTAR) adhered to the tank wall (Figure 1b). A Sony VPL-DX122 LCD projector connected to a Toshiba Portégé Z30-B-10G Ultrabook was used to project the simulated prey. The progressive scanning of the 60Hz LCD screen and the constant lamp output of the projector ensured that the critical flicker frequency of stickleback, thought to be higher than humans (Healy et al., 2013), is unlikely to be an issue here (for full explanation see Künzler and Bakker, 2001, pp 681-682).

To reduce brightness and glare, the projector was placed behind a screen (Solar Control High Reflective Silver Window Film, The Window Film Company UK Ltd, Chesham, UK). The screen also functioned to reduce heat and UV transmission by 77% and 99% respectively. Two webcams (Microsoft LifeCam Cinema), connected to a second laptop (Samsung NP-R780-JT3BUK) were placed outside of the tank, facing the projection wall, to allow for data collection (see Experimental Procedure, below). Webcam 1 (Figure 2.1) was positioned above the waterline and allowed observation of the fish exploring the tank and approaching the projection. Webcam 2 was placed directly below webcam 1 and allowed underwater observation of the fish attacking the simulated prey group.

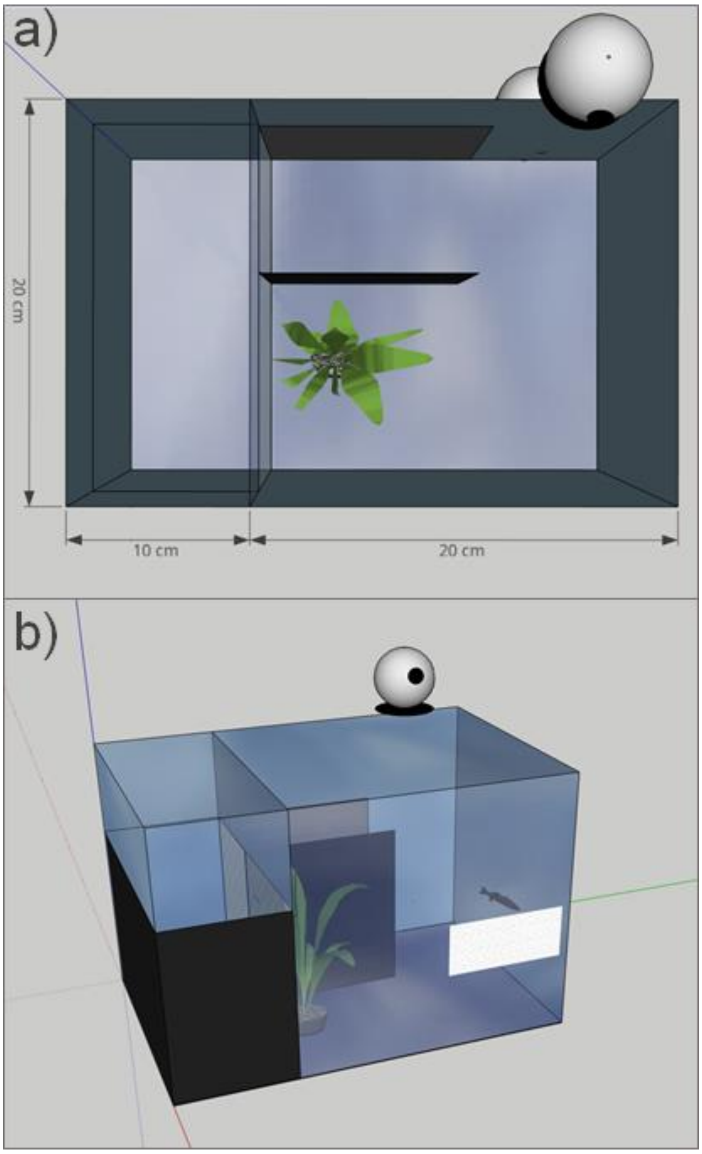

Figure 2.1 A representation of the experimental tank. a) An aerial view with dimensions. The tank was split into a smaller companion area, and a larger focal area. The focal area was further divided into a refuge area and the experimental area, better visible in b) a side view of the experimental tank. The white rectangle at the front of the tank represents the area in which stimuli were presented. Two webcams were positioned, one directly below the other Webcam 1 is visible in both a) and b). Webcam 2 is partly visible in a), and was positioned directly opposite the projection, filming through the glass tank wall.

2.3.3 Simulation of prey

All simulations were carried out using OpenSesame v3.0.7 (Mathôt et al., 2012), using a screen resolution (canvas) of 1360 x 768 pixels. The canvas was coloured an intermediate shade of grey, RGB 129,129,129. N_{group} dots (N_{group} = 16) were positioned on the canvas by selecting pseudorandom integer values from a uniform distribution between x_{min} and x_{max}, and between y_{min} and y_{max} for each dot *i* (see Appendix Table 2.5 for details of parameters used in the simulation). The minimum and maximum values of x and y were chosen to define an active area of the canvas suitable for projection onto the experimental tank, and gave an approximate projected array area of 3 x 7 cm. Each dot had a radius *r* of 7.5 pixels, centred on (x_i, y_i), and a pseudorandom orientation (movement direction, d_i) between 0 and 2π radians. Dots were coloured (c_i) according to whether they were odd or a *distractor* (the remainder of the group). Dots $1 \leq i \leq N_{odd}$ were coloured as specified by shade of the odd dot, and the remainder the shade of the *distractors* (see Table 2.1 for number of odd dots). ‘Dark’ dots were defined as RGB(1,1,1) and ‘light’ dots as RGB 255,255,255. Dots therefore differed from one another in luminance, but not colour. The combination of achromatic stimuli presented through a UV-filter ensured that prey stimuli could not be differentiated on the basis of hues that are invisible to humans (Oliveira et al., 2000; Baldauf et al., 2008). A circular dot shape was chosen to represent the prey. This avoided the assumption that other projected shapes, such as those of natural prey, would be viewed as such by the stickleback.

In each timestep *t*, the position of each dot was updated such that:

$$x_{i(t+1)} = x_{i(t)} + v * \cos(d_i)$$

$$y_{i(t+1)} = y_{i(t)} + v * \sin(d_i)$$

The value of *v* (*v* = 1.5) was selected such that the dots appeared to move smoothly and continuously to a human observer. To ensure that the dots did not move in straight lines, after the position of dots had been altered, their orientation was adjusted such that:

$d_{i(t+1)} = d_{i(t)} + a_{max} * (b_i - 0.5)$, where b is a pseudorandom number between 0 and 1.

Random motion is common in many zooplankton species (Seuront et al., 2003; Komin et al., 2004; Strickler et al., 2005) and the random elements of swimming behaviour will elicit attack from predatory fish (Matsunaga and Watanabe, 2012).

For any dots that left the canvas (where any of $x_i > x_{max}$, $x_i < x_{min}$, $y_i > y_{max}$ or $y_i < y_{min}$), orientation was updated such that $d_{i(t+1)} = d_{i(t)} + \pi$, meaning that they reversed direction and 'bounced' back into the group. This ensured that the group did not become more dispersed during the simulation, mimicking natural groups where compaction is maintained (Seghers, 1974; Magurran and Pitcher, 1987). The simulated dots will henceforth be referred to as 'prey-dots'.

Table 2.1 The 11 possible prey-dot group compositions, including the number of experimental trials (N experiments) per treatment.

Group type	***N* experiments**	N_{odd}	**dark : light**	**Set**
1-odd	16	1	1:15	2
1-odd	15	1	15:1	2
2-odd	15	2	2:14	1
2-odd	19	2	14:2	1
3-odd	17	3	3:13	2
3-odd	15	3	13:3	2
4-odd	21	4	4:12	1
4-odd	12	4	12:4	1
equal	35	8	8:8	1 & 2
homogenous	16	0	16:0	1 & 2
homogenous	16	0	0:16	1 & 2

2.3.4 Experimental procedure

The experimental tank (Figure 2.1) was filled to a depth of 13 cm of system water, with an olfactory cue added to stimulate predatory feeding behaviour (Johannesen et al., 2012). The olfactory cue was made by defrosting 2 blocks of Gamma brand frozen *Daphnia* in 20ml system water. The *Daphnia* were then strained through a fine mesh net to ensure that the cue contained no solids. Three non-experimental fish were carefully netted into the companion area (Figure 2.1a) 5-10 min before experimentation commenced. Companion fish had visual and olfactory contact with the focal fish in both the refuge area (Figure 2.1a) and experimental area (Figure 2.1b), but their view into the experimental area was partially obstructed by a plastic plant. Companion fish were not used as test fish.

At the start of each trial, the focal fish was netted from the holding tank into the refuge area, and the prey simulation was started. Within a single trial a fish was presented with up to 7 arrays (prey-dot groups). Fish were allowed 20 min to attack the first group of prey-dots within a trial. For each subsequent prey group, fish were allowed up to 10 min to attack. The additional 10 min of time to attack the first group was to allow for acclimatization and tank exploration. If an individual continued to show interest in the stimuli, by attacking prey-dots within the allotted time, it was presented with up to 7 treatments out of a possible 11 (Table 2.1). In a first set of trials (N=35 fish) prey-dot groups were homogenous (0-odd, 16 dark or 16 light prey-dots), equal (8-odd), 2-odd and 4-odd (Table 2.1). In a second set of trials (N=34 fish) prey-dot groups were homogenous, equal, 1-odd and 3-odd (Table 2.1). Groups in both sets were presented in a random order.

Each individual trial ended either when the fish made an attack towards a prey-dot, or when the allotted attack time expired. As the fish attacked, the experimenter froze the moving prey-dots by pressing the spacebar, then used the mouse to click at the position of the attack. The coordinates and phenotype of each prey-dot, in addition to the coordinates of the mouse click, were recorded for use in analysis. If the experimenter froze the array > 0.45 sec before or after the fish made contact with the screen this was noted as a failed trial and the experimenter moved on to the next prey-dot group. 0.45 sec was equivalent to a timescale where the dots had visually (to a human observer) shifted position. This occurred on 93 out of 339 occasions in total. The proportion of these occurrences were similar across each treatment type, with no significant difference between the greatest number of occurrences (9/27 trials in the 4 light:12 dark array) and the fewest (4/27 trials in the 3 dark:13 light array; proportion test: x = 1.621, p = 0.203).

At the end of the trial, fish were measured to the nearest 0.1 mm (standard length) using dial callipers before being put back in their system tank. A total of 87 fish were tested, however 18 fish did not make a first attack within 20 min and 2 fish were removed from analysis due to experimenter error, resulting in a final sample size of n=67, (standard length 28.4-51.7 mm), see Table 2.1 for breakdown of sample sizes by treatment. A total of 197 attacks were made, with a mean of 2.95 attacks per fish.

2.3.5 Data Analysis

Data were analyzed in R v.3.3.1 (R Development Core Team, 2015). A binomial test was used to assess whether the proportion of attacks made towards light and dark targets differed from random expectation in the equal ratios treatment. As there was no significant deviation from random (13 attacks to dark, 21 attacks to light; binomial test, p = 0.230), fish could be said to express no particular preference for light or dark dots, so data were pooled by the number of odd individuals for all further analysis.

Generalised linear mixed effects models (package lme4 1.1–12; Bates et al. 2015) were used to explore the effects of *oddity* status (odd or not), number of odd individuals (treatment), position (centre or edge of the group) and local density (distance to the nearest neighbour), and their interactions on whether or not a dot was targeted (target = 1, not target = 0). Trial number nested within fish ID was added as a random effect (random intercepts) to account for the repeated measures nature of the data (multiple dots per trial and multiple trials per fish). An observation-level random effect (random intercepts) was also added to account for over dispersion in the data (Harrison, 2014). There was no collinearity between the main effects ($VIF \leq 2.5$). Body length and the site from which fish were sourced were initially checked and found to have no effect on target choice (Appendix Table 2.6). Both were left out of further analysis to focus on variables of interest.

We identified a set of candidate models, including all possible combinations of pairwise interactions between the four variables, plus the model including all three-way (and lower order) interactions and the model containing the 4-way interaction (and all lower order interactions). Every model contained the 4 main effects. This gave a total of 66 candidate models. We ranked these models by AIC_C scores and assigned them Akaike weights (ω_m) based on these scores (package MuMIn 1.40.0, Barton, 2017). All models with AIC_C within 2 of the best model AIC_C ($\Delta AIC_C \leq 2$) were included in the top model set. We calculated full averaged estimates for each variable and interaction appearing in the top model set (i.e. model-weighted averages of predictor estimates over all top set models including those that did not contain the predictor).

We also calculated the relative importance of explanatory variables (ω_p; the sum of Akaike weights of all top set models containing the variable). We reanalyzed our data using the mean distances to the 2-4 closest neighbours in place of the distance to the nearest neighbour and found the results to be broadly consistent (Appendix Table 2.7).

Further binomial tests were used to assess whether fish attacked odd individuals more often than expected by chance given their frequency in the group, and a proportion test was used to assess whether edge individuals were attacked more often than expected by chance, given the likelihood of an individual being defined as ‘edge’.

2.4 Ethical statement

Experiments were approved by the University of Hull's School of Biological, Biomedical and Environmental Sciences and Faculty of Science and Engineering ethical review committees before commencement (reference numbers U094 and U095), and followed the Association for the Study of Animal Behaviour Society Guidelines for the treatment of animals in behavioural research and teaching (ASAB/ABS, 2018). Care was taken to minimize stress to the experimental fish by the provision of companion fish and refuge areas during the experiment, and by careful handling.

2.5 Results

All models in the top model set (Table 2.2) contained an interaction between *oddity* status and the number of odd individuals in the array on the likelihood of a particular dot being attacked (Table 2.3). Odd individuals were more likely to be attacked, but only when there were 1 or 2 (rather than 3 or 4) in the array (binomial tests: Table 2.4; Figure 2.2a). The models also highlighted that edge individuals (Table 2.3; proportion test: X^2=63.874, df=1, p<0.001; Figure 2b) were attacked more often than those in the centre of the group. These results were broadly robust to the choice of nearest neighbour distance as a measure of local density (Appendix Table 2.7). However, including 3 or 4 neighbours (but not 2) in the measure of local density showed that those with higher average nearest neighbour distances (low local density, or more isolated individuals) were more likely to be attacked (Appendix Table 2.7 b and c; Figure 2.2c).

Table 2.2 The top model set according to AIC, drawn from models including and excluding interaction terms. Terms in bold are significant at p<0.05 assessing the impact of individual terms in the model (Table 2.3 & Appendix Table 2.8).

Rank	Single variable terms	Interaction terms	df	AIC_C	ΔAIC_C
1	**Oddity status** Number odd **Position** Local density	**Oddity status * number odd** Position * local density	10	1274.018	0
2	**Oddity status** Number odd **Position** **Local density**	**Oddity status * number odd**	9	1275.100	1.081
3	**Oddity status** Number odd **Position** Local density	**Oddity status * number odd** Oddity status * local density Position * local density	11	1275.280	1.261
4	**Oddity status** Number odd **Position** Local density	**Oddity status * number odd** Number odd * local density Position * local density	11	1275.756	1.737
5	**Oddity status** Number odd **Position** **Local density**	**Oddity status * number odd** Oddity status * position Position * local density	11	1275.930	1.912
6	**Oddity status** Number odd **Position** Local density	**Oddity status * number odd** Position * local density Position * number odd	11	1276.011	1.993

Variance and standard deviation of random effects was <0.001 in the best-fitting model

Table 2.3 Model-averaged parameters from the GLMM output with attack status (target or not) as the response variable.

Fixed term	**β**	**95% CI**	**ω_p**	**Z**
(Intercept)	-3.883			
Position	**1.281**	**0.865, 1.697**	**1**	**6.033**
Local density	-0.104	-0.560, 0.352	1	0.446
Number odd	0.072	-0.031, 0.175	1	1.366
Oddity status	**1.049**	**0.453, 1.646**	**1**	**3.448**
Oddity * number odd	**-0.125**	**-0.234, -0.015**	**1**	**2.234**
Position * local density	0.309	-0.054, 0.805	0.82	1.262
Oddity * local density	0.019	-0.146, 0.378	0.16	0.273
Local density * number odd	0.001	-0.018, 0.031	0.13	0.169
Position * _oddity_	0.014	-0.589, 0.820	0.12	0.105
Position * number odd	< 0.001	-0.063, 1.697	0.11	0.049

Full model-averaged estimates (β), 95% confidence intervals (CIs), relative importance (ωp) and Z are shown for all models appearing in the top model set (ΔAICC ≤ 2). Predictor CIs that do not overlap with zero are shown in bold. Candidate models: 66, top set models: 6 (see Table 2.2).

Table 2.4 Binomial test output where the number of attacks to odd individuals were compared to what would be expected if odd shaded dots were targeted at random, with respect to overall group size and baseline probability (chance). Significance level is indicated by terms in bold, with * for $p<0.05$, ** for $p< 0.01$ and *** for $p<0.0001$***.

Treatment	**# trials odd targeted in**	**total # trials**	**Expected probability**	**p**
1 odd	9	31	0.063	**<0.001 ****
2 odd	9	34	0.125	**0.026 ***
3 odd	9	32	0.188	0.139
4 odd	11	32	0.25	0.154

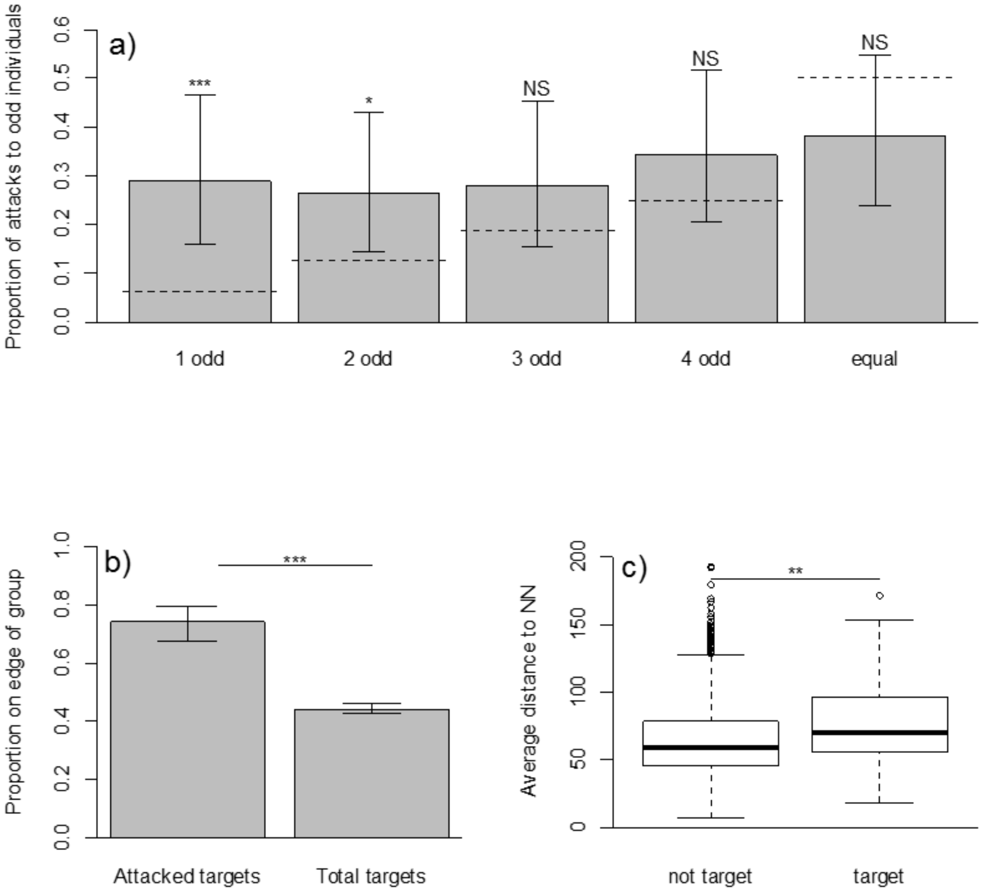

*Figure 2.2 The proportion of attacks made to odd targets at different group compositions, dashed lines signify the point at which attacks would be considered non-random; b); the proportion of attacked targets that were positioned on the edge of the group, compared to the proportion of potential targets that were positioned on the edge of the group; c) the mean distance to the 3 nearest neighbours for dots which were targeted and those which were not (Appendix Table 2.7). * signifies p<0.05, ** p< 0.01 and *** p<0.0001***, non-significance is indicated by NS. For parts a) and b) error bars represent 95% confidence intervals and were calculated using a modified Wald method from Agresti and Coull (1998).*

2.6 Discussion

Using luminance *oddity*, we have validated the use of computerised stimuli to study the *oddity effect*. We were able to demonstrate preferential targeting of a minority phenotype, in line with the *oddity effect* (Ohguchi, 1978; Penry-Williams et al., 2018). 2D arrays were attacked as you would expect if they were 3D, confusing prey group, with preferential targeting of the edges and low density regions (e.g. Hirsch and Morrell, 2011; Duffield and Ioannou, 2017). Other studies have used virtual stimuli to successfully examine the *confusion effect* (Scott-Samuel et al., 2015; Hogan et al., 2017b), marginal predation (Duffield and Ioannou, 2017), the coordination of prey movement (Ioannou et al., 2012; Lemasson et al., 2016) and the targeting success of humans predating odd prey (Ruxton et al., 2007). However, to our knowledge, this is the first demonstration of the *oddity effect* using a naïve, non-human predator preying on computerised prey.

The predatory response of fish to the 2D prey group adds to the work validating the use of virtual prey for studying visually mediated predation (Ioannou et al., 2012; Woo et al., 2016; Duffield and Ioannou, 2017; Ioannou et al., 2019). We found that individuals on the periphery of the group were significantly more likely to be targeted than those in the centre. This aligns with what would be expected of a pursuit predator attacking a prey group (Hirsch and Morrell, 2011), and with studies examining marginal predation in relation to *confusion effect*s (Duffield and Ioannou, 2017). Targets were significantly more likely to be further away from their nearest neighbours, i.e. they had lower local density, or were more isolated within the group. These findings are contrary to the idea that denser regions of a group attract attention due to higher conspicuousness (Milinski, 1977; Ioannou et al., 2009), but in line with findings that show increased risk to prey at lower local densities (Milinski, 1977; Ioannou et al., 2009).

Detection and selection occur at different stages of the predation process. Fish may be initially drawn to denser regions of the group at the detection stage but choose to target less dense (and less confusing) regions at the attack stage (Milinski, 1977). While we did not measure success, evidence suggests that attacks are more successful when local prey density is lower (stickleback preying on *Daphnia*; Ioannou et al., 2009) or prey individuals are isolated from the group (geckos *Eublepharis macularius* and marmosets *Callithrix jacchus* preying on mealworms, Schradin, 2000). Consequently, a targeting preference for less dense regions can be considered a strategy for overcoming the *confusion effect*.

Attacking dense regions is more perceptually challenging and therefore takes more focus, at the expense of awareness of surroundings. Stickleback are less likely to notice a predator when attacking a dense swarm, and when they are exposed to a predator before being presented with a prey group, they will target areas of lower local density (Milinski, 1984). Bees have increased difficulty finding a target flower within a group of higher density *distractor* flowers (Spaethe et al., 2006). In humans, increased density, or visual clutter, contributes to crowding effects, impairing the identification of targets (Whitney and Levi, 2011), although this phenomenon can be overcome if targets are salient because they are visually distinct i.e. they are odd (Põder, 2002).

Odd prey-dots were significantly more likely to be targeted when groups contained 1 or 2 odd prey-dots, but not when there were 3 or 4. These results suggest that joining a majority unmatched group may not necessarily increase predation risk for minority phenotype individuals, above a low threshold. However, we cannot say whether this threshold is an absolute number or proportion as we only tested a single group size of 16 individuals. Landeau and Terborgh (1986) found that when 1 or 2 odd coloured minnow, but not 4, were present within a prey group of 8, bass were significantly more likely to make a successful attack to any group member, odd or otherwise. This effect did not scale up to group sizes of 15, where no 5 minute trials ended in a successful attack, and thus the question of absolute or proportional thresholds could not be answered. In longer experimental trials, lasting 24 hours, Theodorakis (1989) demonstrated bass preferentially targeting size-odd minnow below a threshold of 5, but again this was only in a single group size of 30.

Fish are commonly used to study the *oddity effect*, however a diverse array of animal species respond to digitally generated stimuli (e.g. blue jays *Cyanocitta cristata*, Bond and Kamil, 2002; baboons *Papio papio*, Fagot et al., 2009; chameleons *Chamaeleo chamaeleo*n, Katz et al., 2015; jacky dragon *Amphibolurus muricatus*, Woo et al., 2016) and therefore computerised stimuli to study *oddity*, and other aspects of visual predation are applicable across species. Computerised stimuli form the foundation of studies of attentional capture in experimental psychology (Bundesen and Habekost, 2008) but little is known about attentional capture in other species, particularly fish. Adaptations of the present methodology could be used to address the dearth of research in this area.

Computerised stimuli appear to be a viable and practical method for studying *oddity effect*s, but there is still much to learn about when and why *oddity effect*s occur. While we have demonstrated a preference for odd targets at a low threshold within a group, we cannot make conclusions about what drives the preference we have observed here. The targeting of odd prey may have resulted from attentional capture by odd targets, or because targeting odd prey reduces *confusion effect*s. Further work, using a similar methodology to that presented here, could be used to establish the threshold of 'useful' *oddity*, i.e. *oddity* that improves attack success, and how this interacts with prey group size.

We propose that the use of computerised ‘prey’ is an improved method for studying *oddity effect*s, for the following reasons:

1. Digital stimuli are highly controllable and reduce the potential for confounding factors.
2. Ethical practice is improved because the number of live prey required for experiments are reduced.
3. Once written, code can be shared and reused, greatly improving experimental efficiency and reproducibility.

2.7 Appendix

Table 2.5 Parameters used in the simulation

Parameter	**Description**	**Values**
N_{odd}	Number of odd individuals	$0 \leq N_{odd} \leq 8$
N_{dist}	Number of *distractor* individuals	$8 \leq N_{odd} \leq 16$
N_{group}	Total group size (=$N_{odd} + N_{dist}$)	16
c_i	Shade of dot *i*	‘dark’ or ‘light’
x_i	x-coordinates of dot *i*	$x_{min} \leq x_i \leq x_{max}$
y_i	y-coordinates of dot *i*	$y_{min} \leq y_i \leq y_{max}$
x_{min}	Minimum value of x-coordinates (pixels)	200
x_{max}	Maximum value of x-coordinates (pixels)	680
y_{min}	Minimum value of y-coordinates (pixels)	200
y_{max}	Maximum value of y-coordinates (pixels)	384
r	Radius of dots (pixels)	7.5
d_i	Orientation (movement direction) of dot *i* (radians)	$0 \leq d_i \leq 2\pi$
v	Velocity (pixels/timestep *t*)	1.5
a_{max}	Maximum rotation (radians)	0.9
t	Timestep (t_{max} = 50,000)	

Table 2.6 GLMM including standard body length of fish and the site they were sourced from. Terms in bold are significant at p<0.05.

Fixed term	Est.	Std. Error	Z	P
(Intercept)	-3.450	0.694	-4.973	<0.001
Oddity status	0.373	0.164	2.282	**0.023**
Position	1.235	0.184	6.724	**<0.001**
Local density	0.177	0.071	2.512	**0.012**
Body length	0.000	0.017	0.028	0.978
Site	-0.102	0.204	-0.497	0.619

Table 2.7 Model-averaged parameters from the GLMM output with attack status (target or not) as the response variable, and incorporating mean distance from each dot to its a) 2 nearest neighbours; b) 3 nearest neighbours and c) 4 nearest neighbours.

Fixed term	β	95% CI	ω_p	Z
a) 2 nearest neighbours				
(Intercept)	-3.801	-4.263, -3.339		
Position	**1.193**	**0.806, 1.579**	**1**	**6.051**
Local density	0.180	-0.057, 0.417	1	1.489
Number odd	0.073	-0.029, 0.174	1	1.405
Oddity status	**1.043**	**0.440, 1.646**	**1**	**3.390**
Oddity * number odd	**-0.123**	**-0.232, -0.015**	**1**	**2.222**
Position * local density	0.021	-0.298, 0.551	0.16	0.209
Local density * number odd	-0.001	-0.033, 0.019	0.16	0.182
Oddity * local density	0.010	-0.204, 0.335	0.15	0.171
Position * *oddity*	0.017	-0.587, 0.822	0.15	0.119
Position * number odd	-	-	-	-
b) 3 nearest neighbours				
(Intercept)	-3.783	-4.260, -3.306		
Position	**1.104**	**0.675, 1.533**	**1**	**5.047**
Local density	**0.288**	**0.037, 0.539**	**1**	**2.249**
Number odd	0.075	-0.029, 0.179	1	1.417

Oddity status	**1.027**	**0.400, 1.653**	**1**	**3.212**
Oddity * number odd	**-0.123**	**-0.232, -0.014**	**1**	**2.221**
Local density * number odd	-0.011	-0.050, 0.009	0.54	0.736
Oddity * local density	0.022	-0.168, 0.509	0.2	0.261
Position * local density	0.008	-0.353, 0.504	0.13	0.104
Position * *oddity*	0.034	-0.551, 0.901	0.1	0.193
Position * number odd	0.003	-0.049, 0.100	0.1	0.177
c) 4 nearest neighbours				
(Intercept)	-3.787	-4.272, -3.301		
Position	**1.047**	**0.595, 1.499**	**1**	**4.542**
Local density	**0.372**	**0.108, 0.635**	**1**	**2.766**
Number odd	0.079	-0.026, 0.184	1	1.467
Oddity status	**1.035**	**0.413, 1.657**	**1**	**3.263**
Oddity * number odd	**-0.125**	**-0.234, -0.016**	**1**	**2.254**
Local density * number odd	-0.020	-0.055, 0.004	0.81	1.207
Position * number odd	0.005	-0.041, 0.109	0.15	0.268
Oddity * local density	0.018	-0.204, 0.469	0.14	0.233
Position * *oddity*	0.037	-0.453, 1.008	0.13	0.224
Position * local density	-0.004	-0.475, 0.388	0.1	0.062

Full model-averaged estimates (β), 95% confidence intervals (CIs), relative importance (ω_p) and Z- are shown for all models appearing in the top model set ($\Delta AIC_C \leq 2$). Predictors with CIs that do not overlap with zero are shown in bold. Candidate models: 66, top set models: a) 5 b) 7 c) 6.

Table 2.8 GLMM output for the top model set, with attack status (target or not) as the response variable. Terms in bold are significant at p<0.05.

Fixed term	**Est.**	**Std. Error**	**Z**	**P**
a) model rank 1				
(Intercept)	-3.910	0.242	-16.155	< 0.001
Oddity status	**1.068**	**0.288**	**3.703**	**0.000**
Number odd	0.073	0.052	1.403	0.161
Position	1.301	0.197	6.594	**0.000**
Local density	-0.149	0.205	-0.727	0.467
Oddity * number odd	**-0.125**	**0.056**	**-2.242**	**0.025**
Position * local density	0.376	0.219	1.718	0.086
b) model rank 2				
(Intercept)	-3.813	0.229	-16.620	< 0.001
Oddity status	**1.052**	**0.288**	**3.657**	**0.000**
Number odd	0.072	0.052	1.384	0.166
Position	**1.235**	**0.184**	**6.722**	**0.000**
Local density	0.178	0.071	2.521	**0.012**
Oddity * number odd	**-0.122**	**0.056**	**-2.200**	**0.028**
c) model rank 3				
(Intercept)	-3.895	0.242	-16.090	< 0.001
Oddity status	**1.032**	**0.292**	**3.532**	**0.000**
Number odd	0.073	0.052	1.408	0.159
Position	**1.301**	**0.197**	**6.596**	**0.000**
Local density	-0.196	0.212	-0.926	0.354
Oddity * number odd	**-0.125**	**0.056**	**-2.252**	**0.024**
Oddity * local density	0.116	0.134	0.869	0.385
Position * local density	0.375	0.219	1.712	0.087
d) model rank 4				
(Intercept)	-3.897	0.243	-16.028	< 0.001
Oddity status	**1.068**	**0.288**	**3.704**	**0.000**

Number odd	0.070	0.052	1.352	0.176
Position	**1.301**	**0.197**	**6.593**	**0.000**
Local density	-0.186	0.217	-0.859	0.390
Oddity * number odd	**-0.125**	**0.056**	**-2.242**	**0.025**
Number odd * local density	0.374	0.219	1.709	0.088
Position * local density	0.007	0.012	0.529	0.597
e) model rank 5				
(Intercept)	-3.876	0.263	-14.756	< 0.001
Oddity status	**0.983**	**0.393**	**2.502**	**0.012**
Number odd	0.073	0.052	1.399	0.162
Position	**1.255**	**0.243**	**5.157**	**0.000**
Local density	-0.150	0.205	-0.730	0.466
Oddity * number odd	**-0.125**	**0.056**	**-2.237**	**0.025**
Oddity * position	0.116	0.359	0.321	0.748
Position * local density	0.377	0.219	1.720	0.085
f) model rank 6				
(Intercept)	-3.890	0.277	-14.027	< 0.001
Oddity status	**1.068**	**0.288**	**3.704**	**0.000**
Number odd	0.069	0.058	1.193	0.233
Position	**1.273**	**0.272**	**4.678**	**0.000**
Local density	-0.151	0.206	-0.732	0.464
Oddity * number odd	**-0.125**	**0.056**	**-2.242**	**0.025**
Position * local density	0.377	0.219	1.721	0.085
Position * number odd	0.005	0.035	0.149	0.882

Variance and standard deviation of random effects was <0.001 in the best-fitting model

Chapter 3. Number of prey, not group area or density, drives the preferential targeting of odd prey

3.1 Abstract

Group size and density affect the targeting success of a predator when attacking groups of prey. Larger and denser groups reduce success through *confusion effect*s, where increasing *visual noise* results in decreasing targeting *accuracy*. Predators can potentially reduce the severity of *confusion effect*s by targeting individuals in the group that are phenotypically distinct, the *oddity effect*, but how group features interact with prey *oddity* to affect targeting behaviour is unknown. Stickleback (*Gasterosteus aculeatus*) attacking simulated groups of prey-dots were used to examine how the *oddity effect* was influenced by group size (number of individuals), density and area. We found that number, rather than density or area, drove the targeting of odd prey-dots. Numerically small groups were attacked randomly, while in numerically large groups odd prey-dots were more likely to be targeted than would be expected by chance alone. This has consequences for the grouping decisions of prey: *oddity* may be less costly in smaller groups and the benefits of joining a larger group may be diminished for odd prey. In addition, potential limits to the 'usefulness' of *oddity* were identified.

3.2 Introduction

Being part of a group affords individuals numerous antipredator benefits, including the dilution of individual risk, shared vigilance, the selfish herd effect and the *confusion effect* (reviewed in Krause & Ruxton, 2002; see Box 1 for italicised key terms). The *confusion effect* is thought to result from an overburdened visual system; many items crowding the same receptive fields cannot be processed efficiently (Krakauer, 1995;

Ioannou et al., 2008). The limited capacity of the visual system is characterised behaviourally by higher attack latency (Milinski, 1979), lower attack success (Miller, 1922; Landeau & Terborgh, 1986) and a higher degree of spatial error (Ioannou et al., 2009), when predators are presented with confusing prey groups. To improve the diminished attack success that results from *confusion effect*s, predators can target visually distinct individuals. This is known as the *oddity effect* (Milinski, 1977; Ohguchi, 1978).

Predators will select rare, or odd, individuals when attacking a group (Mueller, 1971; Theodorakis, 1989; Penry-Williams et al., 2018). The preferential selection of common prey types is also observed and the switch to odd prey seems to occur when groups are *confusing* (FitzGerald & Wootton, 1986; Krause & Ruxton, 2002). However it is not known which group features drive the selection of odd prey. Predator *confusion* appears to be enhanced by larger group size (Hogan et al., 2017b), increased density (Milinski, 1977; Kunz et al., 2006) and the morphological (Landeau and Terborgh, 1986) and behavioural (Ioannou et al., 2012) similarity of group members. Odd prey are increasingly targeted when they make up a small minority of an otherwise homogenous group (Chapter 2; Landeau & Terborgh, 1986). However, how other group factors, such as group size and density, influence the selection of odd prey is unknown.

Increasing the number of prey within a group increases predator *confusion*, with larger groups being more challenging for predators to successfully attack (Hogan et al., 2017b). A single bass (*Micropterus salmoides*) predator preying on minnow (*Hybognathus nuchali*) made successful attacks on groups of 2, 4 and 8 but none at 15 (Landeau & Terborgh, 1986). Both geckos (*Eublepharis macularius*) and marmosets

(*Callithrix jacchus*) had greater attack latency when foraging on groups of 20 mealworms (*Tenebrio molitor*) compared to individually presented prey (Schradin, 2000). When prey density is controlled for, the number of prey individuals remains a contributing factor to predator *confusion*. Increasing the number of digital prey within a group was found to increase attack latency in humans (Ruxton et al., 2007). However, once an attack was launched, targeting success (hit-or-miss) was unaffected by group size. In stickleback (*Gasterosteus aculeatus*) preying on *Daphnia,* prey number was found to drive the *confusion effect*, with greater spatial error occurring in groups containing more individuals (Ioannou et al., 2008).

The role of density in predator *confusion* is less clear. Ioannou et al. (2008) discounted group density and area as driving factors behind the *confusion effect*. Humans preying on digital targets (Ruxton et al., 2007) and artificial neural networks (Tosh et al., 2006b) also suggest that the compaction of groups does not enhance *confusion*. However, Ioannou et al. (2009) found that density on a local scale did affect attack success. The spatial error of attacks increased when targets were nearer to their neighbours, i.e. when local density was higher. Scott-Samuel et al. (2015) found density rather than number to be the driving factor behind the *confusion effect* using humans targeting digital prey. Density and number can also act synergistically to reduce the attack success of predators (Hogan et al., 2017b); in humans preying on simulated flocks of starlings the effect of density was greater in larger groups, and vice versa (Hogan et al., 2017b).

Although it has been demonstrated that area does not drive *confusion* (Ioannou et al., 2008) that does not necessarily mean it is entirely unimportant. Cumulative surface area is used as a proxy for pure numerical information, with larger area equating to higher number (mosquitofish *Gambusia holbrooki*, Agrillo et al., 2011). Mosquitofish will use this proxy to make judgements about numerical group size in the context of social (Agrillo et al., 2011) and foraging (Gómez-Laplaza et al., 2018) decisions. This suggests that if the number of individuals is important in *confusion effect*s, then the area of space that a group occupies may also be.

Predators are able to overcome the *confusion effect* by distinguishing prey from their group mates spatially, through isolation (Turesson & Brönmark, 2007), or phenotypically by means of the *oddity effect* (Landeau & Terborgh, 1986). Australian salmon (*Arripis trutta*) targeting mysid swarms (*Paramesopodopsis rufa*) were more successful at capturing prey when in groups, rather than alone (Foster et al., 2001). This was attributed to group members taking different roles, with a lead fish breaking up the densest part of the swarm. Once the group was more dispersed the predators were able to target individual prey. Attacking isolated prey removes the possible negative effects of prey number, area and density. Isolated prey can then be targeted with a greater degree of *accuracy* (Tosh et al., 2006a; Ruxton et al., 2007; Turesson & Bronmark, 2007). Perch (*Perca fluviatilis*) were observed to increase attack success by breaking up groups of roach (*Rutilus rutilus*) and targeting stray individuals (Turesson and Bronmark, 2007). For humans targeting digital prey, stray individuals were at increased risk of successful capture (Ruxton et al., 2007).

The aforementioned *oddity effect* is another strategy that can be used to overcome the challenge of attacking a confusing prey group. The *oddity effect* is evident from both the grouping preferences of prey and the targeting choices, and success, of predators. Fish of similar colour (Rodgers et al., 2010) and size (Krause et al., 1996) will preferentially shoal together. This assortative grouping appears to be stronger when perceived predation risk is high (Krause et al., 1996; Rystrom et al., 2018). Predators preferentially target visually distinct individuals (Almany et al., 2007; Rutz, 2012), and the presence of odd prey increases attack success (Landeau & Terborgh, 1986). In addition to preferential targeting of odd individuals (Ohguchi, 1978), *oddity effect*s may also act to break up the uniformity of the group, increasing the risk to all individuals, rather than just odd targets. Landeau and Terborgh (1986) demonstrated that the presence of odd minnows increased the attack success of bass towards all (not just odd) group members.

Studies into the *confusion effect* have examined the role of number, area and density (Ioannou et al., 2008; Ioannou et al., 2009; Scott-Samuel et al., 2015; Hogan et al., 2017b). The *oddity effect* is conceptually linked to the *confusion effect* (Krause & Ruxton, 2002). Despite this, there has been no direct comparison of how the group features associated with predator *confusion* affect the preferential targeting of odd prey. We use computerised stimuli to manipulate prey number, area and density to observe how these variables influence the selection of odd targets. We exploit the propensity of stickleback predators to target odd prey (Chapter 2; Ohguchi, 1978; Penry-Williams et al., 2018) and predict that they will increasingly target odd individuals when faced with more confusing groups, such as those with higher number and density.

3.3 Methods

Three-spine stickleback (n=150) were sourced from The Carp Co. (Bourne Valley Fish Farm, Kent, UK) in January 2018 and were housed in system tanks in groups of 10. Fish maintenance and the experimental system were identical to those used in Chapter 2, so only a summary of the experiment is presented here. A focal fish was netted into the test area of the experimental tank (Chapter 2, Figure 2.1), with 3 companion fish behind a transparent, perforated partition. Fish were presented with back-projected, ‘prey’ groups consisting of dots that moved around in a defined area (Table 3.1). The simulated prey groups were either numerically large (16 prey-dots) or numerically small (4 prey-dots) and each group was presented in a spatially large (covering a large area) or spatially small (covering a small area) array (Table 3.1, Figure 3.1). This allowed for direct comparison of groups that differed in two of the three variables of number, area and density, while holding one constant. For example, the ‘4-small area’ and ‘4-large area’ treatments are of equal number, but differ in area and density, while the ‘4-small area’ and ‘16-small area’ treatments are of equal area, but differ in number and density. *Group types* are hereon referred to using the number of prey dots (4 or 16) followed by ‘-LA’ for large area or ‘-SA’ for small area.

Dots were coloured dark (RGB 1, 1, 1) or light (RGB 255, 255, 255). All prey groups contained a single odd individual of the alternative phenotype to the remainder of the group. All 4 possible size x area treatments were presented to the fish (Figure 3.1), these were counterbalanced so that on half the occasions the dark dot was odd, and light was odd on the other half, giving a total of 8 possible display combinations. Fish were presented with all 8 possible combinations in random order. Fish were allowed 20 minutes to attack the first array and 10 minutes for every subsequent array. If the fish did not attack within this time period, the experiment was terminated and the fish was returned to the holding tanks. When a fish attacked the group, the movement of the array was stopped by the experimenter and the point on the screen that the fish made contact with was selected using the mouse. Targets were identified as the nearest prey-dot to that point, the shade of the target and the coordinates of all prey-dots were recorded.

3.3.1 Calibration of prey-dots

Unlike the observations made in Chapter 2, initial trials indicated here that fish showed a preference for dark dots (background colour RGB 129: 13 attacks to dark, 1 to light; binomial test, $p = 0.002$). Thus, prior to experimentation fish underwent trials that allowed calibration of the background shade, so that there was no preference for either light or dark prey-dots ($n=32$). The arrays presented to fish contained a total of 16 moving prey-dots, with an equal number of light and dark. Background shade was adjusted in increments of 10 from RGB 100, 100, 100, and the shade (light or dark) of the target of the first attack was recorded. Three different shades were tested: RGB 100 (9 attacks to dark, 1 to light; binomial test, $p = 0.021$), RGB 90 (8 attacks to dark, 3 to light; binomial test, $p = 0.227$) and RGB 80 (5 attacks to dark, 6 to light; binomial test, $p = 1.000$). The background shade of RGB 80, 80, 80 was selected for use in experiments.

The general simulation methods are as outlined in Chapter 2, but with some additional parameters (Table 3.1). In order to ensure that the apparent movement speeds of dots in both group sizes were identical, some dots were made ‘invisible’ such that they were coloured the same as the background. From a total *set size* of 20, 4 or 16 prey-dots (N_{invis}) were coloured this way. The size of the group (N_{group}, such that $N_{invis} + N_{group} = 20$) and the area in which they were displayed (A_{val}) were manipulated. A_{val} was used to scale the value of x_{max} and y_{max} as x_{max}/A_{val} and y_{max}/A_{val}. Two ‘small area’ treatments ($A_{val} = 2$) of different number (here, 4-SA and 16-SA) and 2 ‘large area’ treatments ($A_{val} = 1$) of different numbers (4-LA and 16-LA) were simulated. $A_{val} = 2$

confined prey to a quarter of the area of $A_{val} = 1$, thus giving a combination of treatments with equal density but different number and area; equal number but different area and density; and equal area but different number and density (Figure 3.1). In the 'small area' treatment, dots were projected in an area approximately 40.5 x 20.5 mm and in the 'large area' treament, the projection area measured 90 x 50 mm. A total of 121 fish were used, 61 of these made no attack within the first 20 min, resulting in a final sample size of n=60.

Table 3.1 Parameters used in the simulation.

Parameter	**Description**	**Values**
N_{odd}	Number of odd individuals	1
N_{dist}	Number of *distractor* individuals ($N_{group} + N_{invis}$) - N_{odd}	3 or 15
N_{invis}	Number of invisible dots (20 - N_{group})	4 or 16
N_{group}	Total group size (=$N_{odd} + N_{dist}$)	4 or 16
c_i	Colour of dot *i*	'dark', 'light' or 'invisible'
A_{val}	Area value, used to adjust the value of x_{max} and y_{max}	1 ('large area' groups) or 2 ('small area' groups)
x_i	x-coordinates of dot *i*	$x_{min} \leq x_i \leq x_{max}$
y_i	y-coordinates of dot *i*	$y_{min} \leq y_i \leq y_{max}$
x_{min}	Minimum value of x-coordinates (pixels)	200
x_{max}	Maximum value of x-coordinates (pixels)	680
y_{min}	Minimum value of y-coordinates (pixels)	200
y_{max}	Maximum value of y-coordinates (pixels)	384
r	Radius of dots (pixels)	7.5
d_i	Orientation (movement direction) of dot *i* (radians)	$0 \leq d_i \leq 2\pi$
v	Velocity (pixels/timestep *t*)	1.5
a_{max}	Maximum rotation (radians)	0.9
t	Timestep (t_{max})	50,000

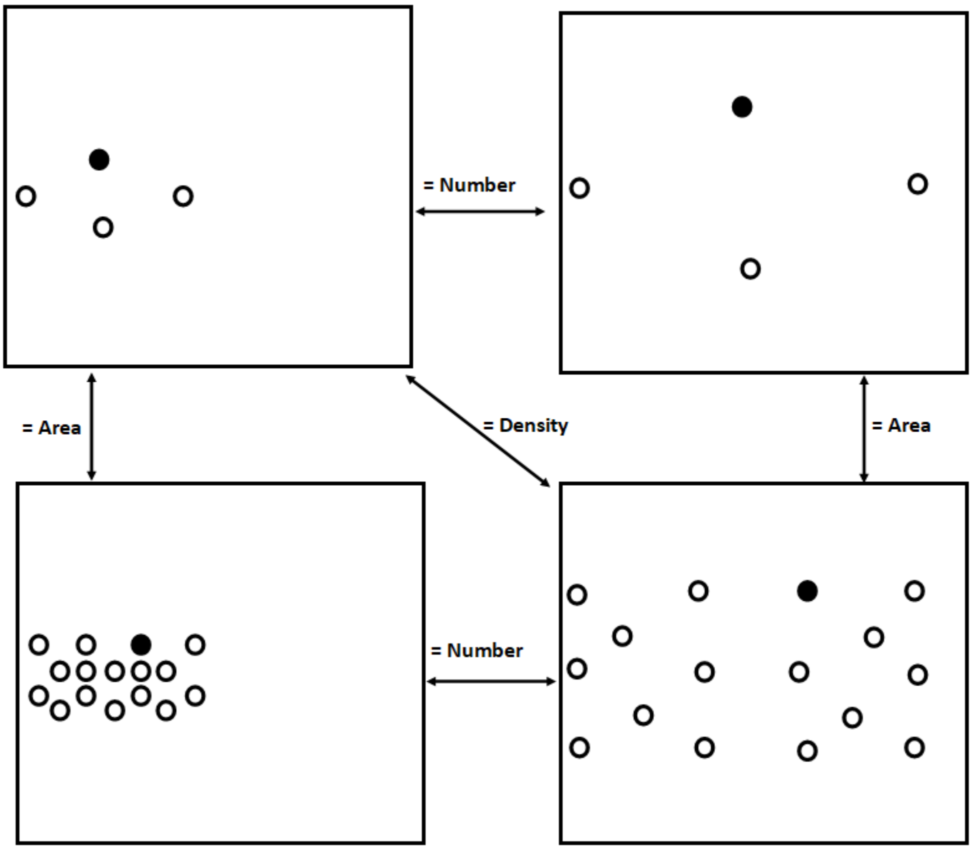

Figure 3.1 Illustration of the simulated prey group types and how they matched and differed in group features. Clockwise from top left: 4-SA, 4-LA, 16-LA and 16-SA. Arrows between the illustrated prey groups indicate the variable (number, area or density) that is kept constant between the two. The other two variables differ.

3.3.2 Data analysis

Data were analysed in R v3.5.0 (R Core Team, 2018). The analysis followed similar methodologies to Chapter 2, assessing risk to individual dots. A generalised linear model with binomial errors was used to assess the effect of *oddity* (odd, uniform), *group type* (4-SA, 4-LA, 16-SA, 16-LA) and their interaction on the proportion of targeted attacks made to a prey-dot (target=1, not target=0). Targets were identified as the prey-dot nearest to where the fish made contact with the screen. Local density (distance to the nearest neighbour) and position in the group were also included as additive effects in the model, as predators may preferentially target both edge individuals (Hirsch & Morrell, 2011) and those in denser areas (Ioannou et al., 2009).

Position was defined as either on the edge of the group (as defined by a position on a vertex of the minimum convex polygon enclosing the group) or in the centre (all other dots).

Trial number nested within fish ID were included as random factors to account for non-independence of dots within a display, and displays targeted by the same individual. Non-significant interactions were removed following Crawley (2005). This model allows exploration of how *oddity* interacts with *group type*, to determine whether or not odd targets are more or less likely to be targeted within groups with different number and area characteristics. A significant interaction between *oddity* and *group type* would indicate that *oddity* is more important in one *group type* than the other. Because *group type* is an amalgamation of two factors, it was necessary to run further models, with re-levelled data, to determine whether interactions resulted from group size or the area occupied to make the comparisons illustrated in Figure 3.1.

In addition, because odd individuals are more likely to be targeted by chance in smaller groups (25% of the time in groups of 4 versus 6.25% in groups of 16), we carried out a series of binomial tests to explore in which treatments odd individuals were targeted more often than would be expected by chance. We also used proportion tests to investigate whether the proportion of attacks to odd dots differed between groups of the same size. Finally, we used binomial tests to assess whether fish were more or less likely than chance to attack any dot in an array (rather than make no attack at all), by comparing the proportion of attacks towards each *group type* against a random expectation of 0.25 (25% of all trials).

3.4 Results

We found no significant difference (i.e. no significant interaction; Table 3.2) in the importance of oddity between the equal number treatments, 4-SA and 4-LA (p= 0.213) or 16-SA and 16-LA (p=0.960). This suggests that group size, rather than area or density, drives the selection of odd prey (Table 3.3). There was a marginally significant interaction when comparing the importance of oddity between the 4-SA and 16-LA treatments, where overall group density was equal (p=0.048), which further indicates a role for group number or area, but not density in determining the risk to odd individuals (Table 3.3). When comparing the equal area treatments, results were conflicting: there was a significant difference in the importance of oddity between the large area group types (4-LA vs 16-LA, p=0.001, Table 3.2) but not the small area group types (4-SA vs 16-SA, p=0.087; Table 3.2).

In groups of 16, odd dots were targeted more often than expected by chance in both the large (Figure 3.2; 9 out of 38 attacks, p<0.001) and small (Figure 3.2; 6 out of 16 attacks, p = 0.005) areas, but there was no difference in the proportion of attacks between the large and small areas ($X^2 < 0.001$, df = 1, p = 1.000). In groups of 4, dots were targeted in line with random expectation in both the large (Figure 3.2; 12 out of 51 attacks, p = 1.000) and small areas (Figure 3.2; 14 out of 41 attacks, p = 0.205) area displays, and again, there was no significant difference between them ($X^2 = 0.794$, df = 1, p = 0.373).

Overall, fish were more likely to attack the 4-LA and less likely to attack the 16-SA than expected by chance (binomial test against 0.25 of all successful trials: 4-LA: 51/156 attacks (32.7%), p = 0.033; 16-SA: 26/158 (16.7%), p = 0.016), while the number of attacks towards 4-SA and 16-SA did not differ from a random proportion of all trials (4-

SA: 41/158 (26.3%), p = 0.712; 16-SA: 38/156 (24.3%, p = 0.926). Unexpectedly, there was no effect of edge/centre position or local density (distance to nearest neighbour) on target choice.

*Table 3.2 Results of the generalised linear mixed effects model assessing the effects of oddity, position, neighbour distance and group type on whether or not a dot was attacked. Significance level is indicated by terms in bold, with * for p<0.05, ** for p< 0.01 and *** for p<0.0001***.grey shading indicates comparisons obtained by re-levelling the model.*

Variable	**Comparison**	**Est.**	**Std. Error**	**z**	**p**
Oddity status	**Not odd v odd**	**1.720**	**0.519**	**3.313**	**<0.001*******
Centre or edge	Centre v edge	-0.165	0.241	-0.687	0.492
Nearest neighbour distance	Continuous	0.100	0.098	1.023	0.306
Group type	16-SA v 16-LA	-0.050	0.302	-0.167	0.867
	16-SA v 4-SA	**1.659**	**0.348**	**4.769**	**<0.001*******
	16-SA v 4-LA	**1.721**	**0.368**	**4.674**	**<0.001*******
	4-LA v 16-LA	**-1.772**	**0.322**	**-5.509**	**<0.001*******
	4-LA v 4-SA	-0.062	0.315	-0.197	0.844
	4-SA v 16-LA	**-1.659**	**0.348**	**-4.769**	**<0.001*******
Oddity status*Group type	16-SA v 16-LA	0.034	0.672	0.050	0.960
	16-SA v 4-SA	-1.117	0.653	-1.709	0.087
	16-SA v 4-LA	**-1.800**	**0.643**	**-2.798**	**0.005****
	4-LA v 16-LA	**1.833**	**0.571**	**3.209**	**<0.001*******
	4-LA v 4-SA	0.683	0.549	1.245	0.213
	4-SA v 16-LA	**1.150**	**0.582**	**1.977**	**0.048***

Table 3.3 Summary of the predictions and outcome of the experiment, comparing equal area, density and number treatments. P-values were obtained from the interaction between oddity and group size in Table 3.1.

Treatment	**Comparison**	**No sig. diff. supports the importance of**	**Sig. diff. supports the importance of**	**Outcome**	**Conclusion**
= Number	4-SA v 4-LA	Number	Area or Density	NS	Number
	16-SA v 16-LA	Number	Area or Density	NS	Number
= Area	4-SA v 16-SA	Area	Number or Density	NS	Area
	4-SA v 16-SA	Area	Number or Density	p = 0.001	Number or Density
= Density	4-SA v 16-LA	Density	Area or Number	p = 0.048	Area or Number

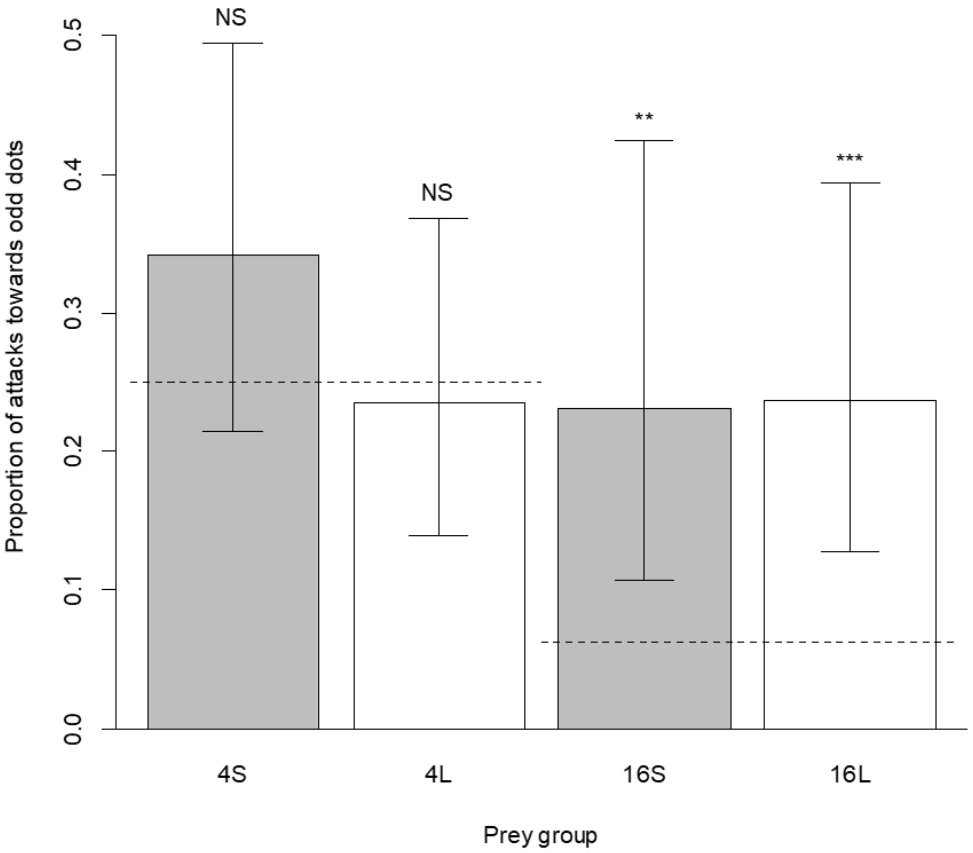

Figure 3.2 The proportion of attacks directed towards odd targets for the 4 different group types. Error bars for proportions were calculated using a modified Wald method (Agresti & Coull, 1998). Dashed lines indicate the expected proportion of attacks towards odd dots if targeting was random with respect to oddity, and asterisks indicate significant deviation from this random expectation.

3.5 Discussion

Together, the results suggest that it is likely to be the number of individuals in a group, rather than the area they occupy or the density they appear in, which drives a preference for attacking odd targets. In line with our predictions, odd prey-dots were attacked significantly more often than random expectation in groups of 16, but not in groups of 4. In the pairwise comparisons of the risk to dots (Table 3.2), no significant interactions between *oddity* status and group size were found for the equal number comparisons indicating the importance of the number of individuals. This is supported by the significant interactions between *oddity* and *group type* in the equal density and one of the equal area treatments, which further suggests a role for the number of individuals. In addition, fish were more likely to refuse to attack 16-SA groups within the allotted time, and least likely to refuse the 4-LA groups. This suggests that, as we predicted, the 16-SA groups were the most confusing (and 4-LA the least), but we are unable to say which feature drove this reduction in attack rate.

Increasing numerical group sizes elicits predator *confusion* (Schradin, 2000), reducing overall attack rate (Landeau & Terborgh, 1986) and increasing spatial targeting error (Ioannou et al., 2008). This is the first demonstration, to our knowledge, that numerical group size is the *confusing feature* (see Box 1. *confusion effect*) that drives the selection of odd prey. Odd prey-dots were not at increased risk within smaller prey groups, suggesting the cost of *oddity* does not occur until groups become sufficiently large. This is also evident in the behaviour of prey, where group size affects shoaling decisions for odd mollies (*Poecilia latipinna* Bradner & McRobert, 2001) and female fighting fish (*Betta splendens* Blakeslee et al., 2009). Mollies prefer larger groups, however they prefer to shoal with a smaller matched group than a large unmatched group (Bradner & McRobert, 2001). The antipredator benefits associated with larger group size (e.g. the dilution of indvidual risk, Krause & Ruxton, 2002) may be diminished by the cost of *oddity* in larger groups. The preferential targeting of odd prey in larger groups, observed here, is in line with neural network models predictions that *oddity* is costlier in larger groups (Krakauer, 1995). However, for humans targeting computerised prey, *oddity* status and numerical group size did not interact to affect the time taken to capture odd targets (Ruxton et al., 2007). To fully understand the risk to odd prey it would be necessary to examine targeting preference alongside attack outcome. Unfortunately, a limitation of the present methodology is that, while robust to the intended choice of attack, adaptions need to be made for finer scale measurements of attack outcome.

It would be expected that areas of low local density (Ioannou et al., 2009) and the edges (Hirsch & Morrell, 2011) of groups would be targeted, as they were in Chapter 2, but this did not appear to be the case here. A possible explanation is that in groups of 16 fish were focused on the targeting of odd prey-dots regardless of their location within the group. For the smaller group size, local density may have been unimportant due to the low group number, and edges were not well defined. Marginal predation preferences have been attributed to encounter, rather than *confusion effect*s. Edges are preferentially attacked because they are encountered first by hunting predators, rather than because doing so reduces *confusion* (Duffield & Ioannou, 2017). In our simulated 2-D prey groups all prey-dots were equally apparent to the fish: when the prey group came into view, the detection stage of predation, fish attacked the most noticeable targets rather than attacking the nearest prey-dot, meaning that preferences for edges were not observed. This finding is, however, at odds with the previous chapter and the observations of Romey et al. (2007).

We found no strong evidence that the density or area of the group drives a preference for *oddity*, although the results do not entirely rule out these factors. Where *oddity effect*s were apparent (in the 16-LA and 16-SA treatments), we found no evidence that increasing the density of the group (by reducing the area that it occupied) led to an increase in the likelihood of odd individuals being targeted. It is possible that odd dots were not targeted more frequently in 16-SA groups because a smaller cumulative surface area resulted in predators estimating a numerically smaller group (Agrillo, 2011). It may also be the case that the selection of odd prey in response to *confusion* simply plateaus, similarly to the 'U shape' of confusion generated by neural network models and further validated using human data (Tosh et al., 2006b)**.** Past a certain point, being presented with a confusing group may simply result in no attacks being made, or imprecise attacks being launched with the intent of targeting any prey within a concentrated area. Predators may be unable to process the visual information to launch an attack due to *confusion effect*s, or choose not to attack because the energy expenditure required is deemed cost ineffective. Landeau and Terborgh (1986) found that bass failed to make any successful attacks, despite the presence of 1 or 2 odd minnow, when prey group size was increased from 8 to 15. This, along with the findings for 16-SA groups, suggests that there is a limit to the usefulness of *oddity* in the amelioration of the *confusion effect*.

If the *oddity effect* initially occurs at the detection stage of the predation cycle then large groups would create greater contrast against an odd individual, increasing its conspicuousness, or *saliency* (Nothdurft, 2000). Odd prey-dots, therefore, would be more conspicuous in groups of 16 than in groups of 4, despite being odd in both contexts. Relative conspicuousness and relative risk have both been shown to impact on group choice decisions. In a comparison of three species of coral reef fish, green chromis (*Chromis viridis*)*,* yellowtail demoiselle (*Neopomacentrus azysron*) and fusilier (*Caesio teres*), only the yellowtail demoiselle preferred shoaling with conspecifics over heterospecifics, avoiding being phenotypically odd (Quattrini et al., 2018). Of the three species, the yellowtail demoiselle was phenotypically most dissimilar, and therefore potentially more conspicuous against the other species. Prey individuals that are larger than their group-mates are more likely to avoid associating in situations where they might be odd (Rodgers et al., 2011; Kimbell & Morrell, 2015b), and more likely to act in a risk-averse manner (Peuhkuri, 1997). Larger prey individuals (Rodgers et al., 2011; Kimbell & Morrell, 2015b), or those that are conspicuous against the wider background (Rodgers et al., 2013), are also more likely to be targeted when odd than small or cryptic individuals. Saliency mapping similar to that outlined in Pike (2018) could be used to quantify conspicuousness of prey within groups, such as the yellowtail demoiselle. However, the transient nature of mobile groups would present challenges.

Areas of contrast, or *oddity*, within a search area have been shown to be salient, through fixation and targeting behaviours, for owls (orientation, Orlowski et al., 2015), zebrafish (colour, Proulx et al., 2014) and archer fish (movement, Ben-Tov et al., 2015). This *saliency* causes items to '*pop-out*' from their surroundings. The '*pop-out effect*' is thus a term used in experimental psychology for a similar phenomenon to the *oddity effect*. However, *pop-out* is generally characterised by the independence of reaction time (attack latency) to *set size* (group size) (Treisman & Gelade, 1980). If the *oddity effect* functioned under the same mechanisms as the *pop-out effect*, one would expect selection of odd prey to be independent of group size, which was not the case here. However, in experimental work examining the *pop-out effect*, individuals are trained to select a particular target, which was not the case in our experiment. Thus, we have not specifically explored the ability of sticklebacks to select odd targets, but the situations where a preference for targeting odd prey dots occurs. Allocating attention to a salient region, or item, within a scene can be explained by the formation of neurological *saliency map*s (Koch & Ullman, 1987). Specific exploration of the *pop-out effect* in trained fish, using a similar methodology, would allow for exploration of the formation of *saliency map*s in non-mammals. In humans this stage of processing occurs in the primary visual cortex (V1) (Li, 2002), a region of the brain that is absent in non-mammals. While *saliency map*s are not well studied in fish, there is evidence that they are computed within the optic tectum (Ben-Tov et al., 2015; reviewed in Zhaoping, 2016), and allow for the *pop-out effect* to operate in a similar way to in humans.

This chapter demonstrates that the *confusing group feature* that drives the *oddity effect* is numerical group size, and that *oddity* is costlier to prey in larger groups. Prey individuals must therefore balance the relative risks of being odd and being a member of a larger group. Larger groups provide additional antipredator protection (Krause & Ruxton, 2002), but these benefits may be diminished by *oddity*. In smaller groups *oddity* does not the increase risk of preferential targeting. Therefore when studying the effect of *oddity* on prey grouping behaviour numerical group size is an important factor to take into consideration. Assortative grouping to avoid *oddity* may not be necessary unless groups are sufficiently large. Finally, there may be limits to the ‘usefulness’ of *oddity*. The decreased rate of attack towards 16-SA groups, but lack of evidence for a further increase in preferential targeting, suggests that the presence of *oddity* is not always enough to overcome *confusion*.

Chapter 4. The oddity effect at the detection stage of the predation cycle

4.1 Abstract

The behavioural consequences of behavioural ecology's *confusion* and *oddity effects* are paralleled by principles of human *visual search*. Specifically, numerical group size, density and the similarity of individuals within a group negatively affect predators at the attack stage of predation. The same features increase human search time, at what would be considered the detection stage of the predation cycle. These reductions in attack success and search performance can be diminished by targeting visually distinct individuals – the *oddity effect* in behavioural ecology and the *pop-out effect* in *visual search*. By employing *visual search* methodology, the *oddity effect* was examined prior to the attack stage, when preferential targeting occurs. Odd targets capture attention in both large and small groups, with target *oddity* easing the challenge of search in numerically large groups. This suggests that preferential targeting of odd prey is at least, in part, a consequence of attentional capture. Spatial results suggest that closer proximity to *oddity* may increase risk to majority type prey, however odd prey capture attention so could also act as decoys. It is possible that both these predictions are true, but sensitive to the limitations and capabilities of both predators and prey within different systems. How the proximity of *oddity* affects risk to majority type individuals should therefore be investigated in a range of predator-prey systems.

4.2 Introduction

A cluttered environment can make *visual search* challenging (Rosenholtz et al., 2005; Xiao & Cuthill, 2016; see Box 1 for italicised key terms). In the context of predator-prey interactions, prey grouping together can increase the perceptual challenge faced by a predator. Many similar-looking individuals reduce the ability of a predator to successfully target and attack individuals within a group (Tosh et al., 2006b). This reduction in attack success is thought to result from cognitive limitations; there is more visual information to be processed, than can be processed (Krakauer, 1995). This is known as the *confusion effect* (Schradin, 2000; Ioannou et al., 2008). The *confusion effect* is thought to be enhanced by the number of individuals (Hogan et al., 2017b), the density of prey (Scott-Samuel et al., 2015), the similarity of group members (Landeau & Terborgh, 1986), and unpredictable (Scott-Samuel et al., 2015), coordinated (Ioannou et al., 2012) but not necessarily protean (Jones et al., 2011) movement. One way that predators are able to overcome the *confusion effect* is by targeting prey that differ on some phenotypic trait to the rest of the group (Landeau & Terborgh, 1986). This is known as the *oddity effect* (Ohguchi, 1978; Penry-Williams et al., 2018).

The behavioural consequences of *confusion* are a decline in successful attacks through increased spatial error (Ioannou et al., 2009), an increased proportion of missed attacks (Tosh et al., 2006b; Ruxton et al., 2007) and/or increased attack latency (Milinski, 1979). The *oddity effect*, from a predatory perspective, is characterised by the presence of odd prey improving attack success (Landeau & Terborgh, 1986; Tosh et al., 2006b; Ruxton et al., 2007) and the preferential targeting of odd prey over those of the majority phenotype (Ohguchi, 1978; Rodgers et al., 2014; Penry-Williams et al., 2018).

The behavioural consequences of the *confusion* and *oddity effect*s can be paralleled with well-studied areas of *visual search* (Tosh et al., 2009). Oddity helps predators to overcome the difficulty of targeting an individual in a large group of similar looking prey (Ruxton et al., 2007). Similarly, the *pop-out effect* removes the challenge of searching a large number of homogenous *distractor* items in *visual search* experiments (Wolfe & Horowitz, 2017). The *pop-out effect* is where a visually distinct *singleton* (see Box 1 *pop-out effect*) – similar to an odd prey individual – differs from the other items in an array – similar to the majority type group members (Ben-Tov et al., 2015) . As a consequence of visual distinctiveness, singletons capture attention and are therefore easy to locate (Wolfe & Horowitz, 2017). In the absence of *pop-out*, there is positive relationship between the number of items in the array, and search difficulty, as quantified by *reaction time* (*RT*; Wolfe, 2016). This can be paralleled to the *confusion effect* (Tosh et al., 2009), where increasing the number of prey individuals within a group increases predator *confusion* (Landeau & Terborgh, 1986; Schradin, 2000). However, *pop-out* is a phenomenon that occurs at the detection stage of the predation cycle (Figure 4.1) and is most commonly studied using static arrays (Põder, 2002; with the exception of Ben-Tov et al., 2015; Orlowski et al., 2015). The *oddity effect* is typically associated with moving prey groups at the attack stage (Milinski, 1977; Ohguchi, 1978; Ruxton et al., 2007; Rodgers et al., 2013; Penry-Williams et al., 2018; Raveh et al., 2019). *Pop-out* is a consequence of attentional capture (Turatto & Galfano, 2000) but exactly why the *oddity effect* occurs is unknown. Odd prey may be targeted because they a) are easier to track and target than other group members, b) attract attention or c) a combination of both these factors.

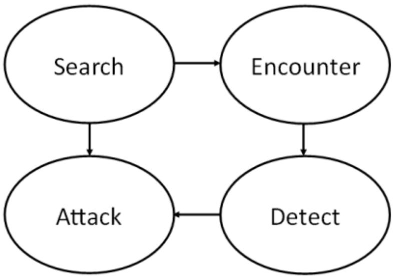

Figure 4.1 The predation cycle, adapted from Jeschke et al.(2002)

Visually distinct prey are, generally speaking, more at risk than other group members (Landeau & Terborgh, 1986; Rodgers et al., 2013; Penry-Williams et al., 2018). However, different individual and group features interact to affect overall risk to group members. For example, in the previous chapter, group size increased the 'risk' to odd prey-dots in line with predictions made by Krakauer (1995). Even when *oddity* is avoided, not all prey within a group are targeted equally (Mathis & Chivers, 2003; Rodgers et al., 2013). It is established that individuals on the edges of groups (marginal predation, Hamilton, 1971) and those which are more spatially isolated, i.e. occupying areas of lower *local density* (Milinski, 1977) are preferentially targeted, possibly to reduce *confusion effect*s. Marginal predation is thought to be driven by the increased chance of a predator encountering edge prey (Duffield & Ioannou, 2017). It is unknown how spatial isolation functions to draw attacks at the encounter/detection stage of predation as areas of greater density are considered more conspicuous and more likely to capture attention (Milinski, 1977; Ioannou et al., 2009).

Tosh et al. (2009) highlighted the potential for *confusion effect* studies to use methodology employed by cognitive psychologists who study *visual attention* and "their own version of *confusion effect*" (Tosh et al., 2009, p473; see Table 1.1 and Box 1 - *visual search*). However, to our knowledge, only one *confusion effect* study employing psychology inspired methodology has also looked at the *oddity effect* (Ruxton et al., 2007). Ruxton et al. (2007) found that a single, grey, odd target within a group of black 'tadpoles' was easier to capture than a black target within a matched group. In the present study we use a similar artificial predator-prey system to investigate the *oddity effect* and features associated with *confusion* and *visual search* difficulty, at the detection stage of the predation cycle (Figure 4.1).

Chapters 1 and 2 examined the *oddity effect* at the attack stage of predation, demonstrating the preferential targeting of odd prey. Odd targets may be preferentially attacked because this helps to ameliorate the *confusion effect*, through ease of targeting, possibly due to attention capture. The selection of targets is considered indicative of *salience* (Mokeichev et al., 2010; Ben-Tov et al., 2018) however, it does not explicitly demonstrate *attention capture*. In human subjects, the time taken to report the presence or absence of a pre-determined *target* can be used to measure the allocation of attention and how challenging a task is (see Box 1 *visual search*; Bundesen & Habekost, 2008). This same experimental paradigm can be used to examine the *oddity effect* at the detection stage of the predation cycle (Figure 4.1) to ask if *oddity* captures attention prior to the attack stage. How this interacts with group features associated with preferential targeting of prey and *confusion*, or search difficulty, can then be investigated. In addition, how search difficulty interacts with *oddity* and the spatial positioning of targets can be explored.

Difficulty of search for a pre-determined *targe*t was manipulated, similarly to 'prey' groups in Chapter 3, through numerical group size (4 prey-dots, or 16 prey-dots) and the area prey-dots move within (large area: LA, or small area: SA; see Box 1 – *group type*). Within these different prey-dot groups, the effect of *oddity* on *attentional allocation* was measured using *response time (RT)*. This allowed the interaction between *oddity*, *attention capture* and position within the group to be investigated at the detection stage of the predation cycle (Figure 4.1). Odd items were either the target or a *distractor*, with an odd *distractor* being referred to as a *foil*.

The objectives were to explore the following questions:

Q1. *Which combinations of numerical group size and spatial area (group type: 4-SA, 16-SA, 4-LA and 16-LA) were most challenging to search (measured as reaction time and response accuracy)?*

'Easy' search is characterised by shorter *RT*s. When looked at alongside *RT*, the *accuracy* of responses can also be indicative of task difficulty, with lower *accuracy* signifying increased search difficulty. The most challenging group will be indicated by the longest *RT*s and lowest response *accuracy*. It is predicted that the largest groups will be most challenging to search. Spatial area could enhance or decrease search difficulty. The crowding of objects can make search more difficult (reviewed in Levi, 2008), however an increased spatial area may naturally take longer to search.

Q2. *How does the presence of oddity affect attentional capture, and thus the difficulty or ease of search (measured as response time, RT)?*

Once search difficulty is established, the effect of *oddity* can be investigated across *group type* (4-SA, 16-SA, 4-LA and 16-LA). Where *oddity* is present, *RT* can be looked at relative to treatments where no *oddity* occurs to determine whether attention is captured by *oddity*. For example, when the target is present and the odd item (target present, target odd: TP/TO; see Box 1 – *dot type*) *RT* should be reduced relative to when the target is present but there is no *oddity* in the group (target present, no oddity: TP/NO). When the target is present but a *foil* is the odd item (target present, foil odd: TP/FO) *RT* should be increased relative to TP/NO.

Q3. *How does the spatial position of the target in relation to the other items in the array, influence difficulty of search?*

‘Easy’ search is characterised by shorter *RT*. Attentional capture reduces *RT* when the target is present and odd (TP/TO), and increases it when a *foil* is the odd item (TP/FO).

The position of the target in relation to other prey-dots, specifically whether it is located centrally, or on the edge, and how close it is to its nearest neighbours may affect *RT*. If search is made easier, or more difficult, by the target position there will be a significant effect of position (centre/edge) and/or local density (nearest neighbour distance) on *RT*. The proximity of the target to the odd prey-dot may affect the time taken to detect the target. If this is the case then a significant effect of target distance to odd prey-dot would be evident for TP/FO groups.

4.3 Methods

4.3.1 Experimental procedure

A computerised, moving ‘prey-dot’ task was created in PsycoPy2 Experiment Builder (v1.85.2, Peirce, 2007; 2009) (Figure 4.2). Dynamic arrays (i.e. moving prey-dot groups) were presented with either dark (RGB -1, -1, -1) majority prey-dots with a light (RGB 1, 1, 1) shaded odd prey-dot, or with light as the majority colour and dark as the colour of the odd prey-dot. All prey-dot arrays were presented on a mid-grey (RGB 0, 0, 0) background. PsychoPy expresses RGB colour space on a scale of -1 to 1 rather than 0 to 255, thus, colours are expressed as deviations from a mid-grey screen (Peirce, 2007; 2009).The task consisted of 576 trials broken down into blocks of 96, to allow for breaks. Between blocks, participants were encouraged to take a break, this is standard in experimental psychology to avoid task-fatigue. In each trial the participant was asked to identify the presence or absence of a pseudo-randomly moving target, a square prey-dot, amongst circular *distractor* prey-dots (also moving pseudo-randomly) in each presented array (Figure 4.2). Participants were instructed to make this decision as quickly and accurately as possible, using a two-alternative-forced-choice (2-AFC) key press responses. In a 2-AFC response, one key on the computer keyboard is assigned to indicate the presence of the target, and the other the absence of the target. The assigned keys were switched for half the participants. In each trial, participants were presented with 4 or 16 prey-dots that moved within a large or small area on the screen (Figure 4.2). Numerical group size and array area were chosen to influence search difficulty. In the absence of *oddity*, many items were expected to be more challenging to search than fewer items (Bundesen & Habekost, 2008). Array area manipulated both the spatial area the group took up and the crowding of prey-dots (nearest neighbour distance). It was unknown whether a dispersed group over a larger search area (LA) or a compact group within a small area (SA) would be most challenging. LA and SA trials were presented as separate experimental blocks as is standard practice in experimental psychology.

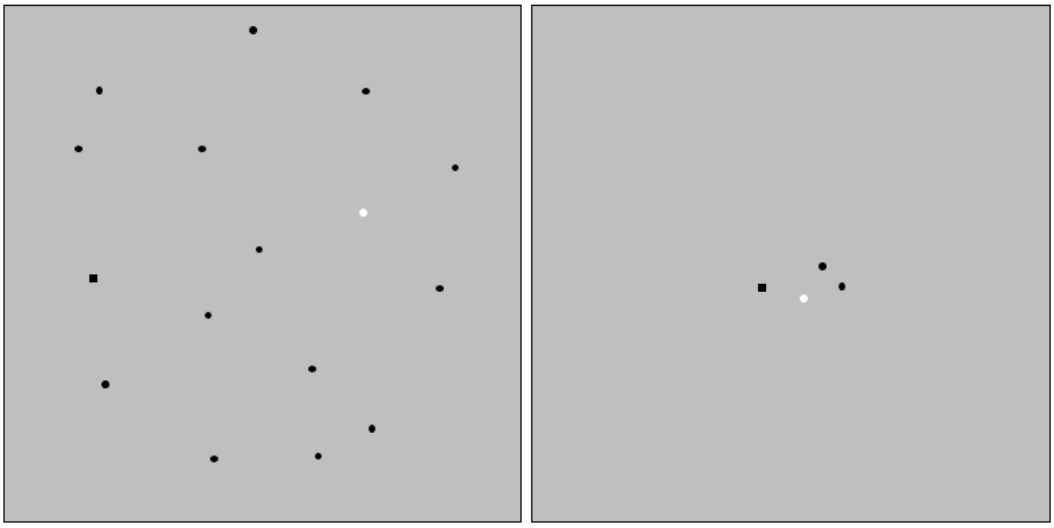

Figure 4.2 Representation of a 16-LA group (left) and a 4-SA group (right). Prey-dots (each 0.35 cm in diameter) moved within an area of 28 x 28 cm for LA, and within 4 x 4 cm for SA. This diagram shows a present target (a black square) with an odd foil (white circle). The remaining distractors are black circles.

Within blocks, arrays were presented in a random order. It was necessary to balance the trials in such a way that the human subjects could not attempt to predict the correct response (Table 4.1). Therefore, in each trial, the target was equally likely to be present or absent, and the odd item was either absent or presented as a circular *distractor* (a *foil*), or as the target. As a result, five factors influenced the appearance of the prey-dot group, these were the five possible combinations of target and odd item presence and identity used in the analysis (Table 4.1). A practice block of 20 trials was provided prior to the start of the experiment.

Table 4.1 The factors of array appearance and the levels within those factors. Number of repetitions per block are given in parenthesis.

Factor	**Levels**
Array area	Large (288), small (288)*
Majority colour, odd colour	Dark, light (48) / light, dark (48)
Oddity status	Foil (40), target (16), none (40) **
Numerical group size	4 (48), 16 (48)
Target status	Absent (48), present (48)

*presented as separate experimental blocks

** Sample sizes appear unbalanced here due to the necessity of balancing the number of present/absent trials within each block.

All stimuli were viewed at 60 cm from a Dell Triniton monitor. Each individual trial began with a white fixation cross, presented at the centre of the screen for 0.5 sec. The fixation cross then disappeared, and 0.5 sec later was replaced by the dynamic (as opposed to static) array (see below for details of the movement simulation). If the participant failed to make a response within 2.5 sec, the trial timed out and the next trial was initiated automatically. Thirty-one participants were recruited to the experiment, and all completed the full set of 576 trials, but data for 2 participants was removed from analysis because their overall *accuracy* was below 70%, resulting in a final sample size of n=29. Participant responses (present/absent), the time to make the response (*RT*) and the X and Y coordinates (position) of each prey-dot were recorded for use in analysis.

4.3.2 Simulation of stimuli

The simulation of the stimuli closely followed that of Chapters 2 and 3, and so is only briefly described here. Each prey-dot *i* was pseudo-randomly positioned on a canvas of 1280 (w) x 1024 (h) pixels, between $-x_{max}$ and $+ x_{max}$, and $- y_{max}$ and $+ y_{max}$, where (0,0) represents the centre of the canvas and the position of the centre of the dot is given by (x_i, y_i). For the LA trials, x_{max} and y_{max} took values of x_{max} = w*0.5 and y_{max} = h*0.5, and for the SA trials, x_{max} = w*0.05 and y_{max} = h*0.05. Each prey-dot had a radius (if a circular *distractor*) or dimensions (if the square target) of 10 pixels and a pseudorandom orientation (movement direction, *d*i) of between 0 and 2π radians. Prey-dot shade (dark or light) was determined as described above.

The movement of the prey-dots used the same method as in Chapter 2. In each timestep the dot moved v=1 pixels in direction d_i, after which its orientation was updated by a pseudorandom value between $-a_{max}$ and a_{max} radians (a_{max} =0.5) to ensure that prey-dots did not move in a straight line. For any prey-dots that left the canvas, their direction d_i was reversed such that they ‘bounced’ back into the group. Each group was displayed for 2.5 seconds or until the participant pressed a key to indicate the presence or absence of the target. The array was then replaced by the fixation cross before the next trial began. The speed (in seconds) and *accuracy* (correct/incorrect identification of the target presence/absence) of the key press, and the position and identity (colour, odd status, target status) of every prey-dot at the moment of the key press was recorded after each trial.

4.3.3 Data analysis

Data were analysed in R v.3.5.0. (Bates et al., 2014; R Development Core Team, 2015). For analysis, the number of items and area variables were combined into a single factor with 4 levels of *group type* (4-LA, 4-SA, 16-LA, and 16-SA). Similarly, the target presence/absence and identity of the odd dot were combined into a single variable with 5 levels of *dot type* (Table 4.1).

Table 4.1. The combined 'dot type' codes used for the target presence/absence and identity of the odd item variables.

Target presence	**Identity of odd prey-dot**	**Dot type***	**Number of times represented in block of 96 trials ****
Present	Target odd	TP/TO	16
Present	Foil odd	TP/FO	16
Present	No oddity	TP/NO	16
Absent	Foil odd	TA/FO	24
Absent	No oddity	TA/NO	24

*Key to *dot type* code: The first two letters define the presence or absence of the target (T): P = Present, A = Absent. The second two letters define the identity of the odd dot (O): T = Target odd, F = Foil odd, N = No *oddity*.

** Sample sizes appear unbalanced here due to the necessity of balancing the number of present/absent trials within each block.

To investigate the effect of numerical group size and spatial area on search difficulty (Q1), data was subset by *dot type*. Generalised linear effect models with gamma errors and an identity link (Lo & Andrews, 2015) were used to investigate the effect of *group type* on *reaction time (RT)*. The same framework was used to analyse response *accuracy* (correct/incorrect) but with generalised mixed effects models with binomial errors. In both analyses subject ID was added as a random effect to account for multiple responses per participant and models were relevelled to give comparisons across all *group types*.

To investigate the effect of *oddity* on search difficulty (Q2), data were subset by *group type*. Generalised linear effect models with gamma errors, an identity link (Lo & Andrews, 2015) and subject ID as a random effect were used to investigate the effect of *dot type* on RT. Again, models were relevelled to give comparisons across all *dot types*.

To investigate how the spatial position of the target influenced search difficulty (Q3) only target present (TP) data from the numerically larger group of 16 prey-dots were analysed (spatial position is relatively uniform between individuals in a group of 4). Spatial position data was defined at the point of keypress, i.e. the point at which the participant reported target detection. Data were subset by *dot type*. For TP/TO and TP/NO, generalised linear effect models with gamma errors and an identity link (Lo & Andrews, 2015) were used to investigate the effect of target position (centre/edge) and the distance of the target to its nearest neighbour (target NN distance) on *RT*. The same analysis was carried out for TP/FO but with the additional variables of odd prey-dot position (odd position), the distance of the odd prey-dot to its nearest neighbour (odd NN distance) and the distance from the target prey-dot to the odd prey-dot (target distance to odd) on *RT*.

4.4 Results

4.4.1 Q1. Which combinations of numerical group size and spatial area (4-SA, 16-SA, 4-LA and 16-LA) were most challenging to search?

The least challenging searches, with the shortest RTs, were observed in the 4-SA groups, followed by 16-SA and then 4-LA (Figure 4.3). Searches were most challenging, with the longest RTs (Figure 4.3, Table 4.2) and lowest accuracy (Figure 4.4, Table 4.3), in the 16-LA group. Increasing both group size and area/density increased reaction time (Figure 4.3, Table 4.2, Table 4.3) and decreased accuracy (Figure 4.4). There were, however, no differences in accuracy between 4-SA and 16-SA in the TP treatments (Figure 4.4, Table 4.3).

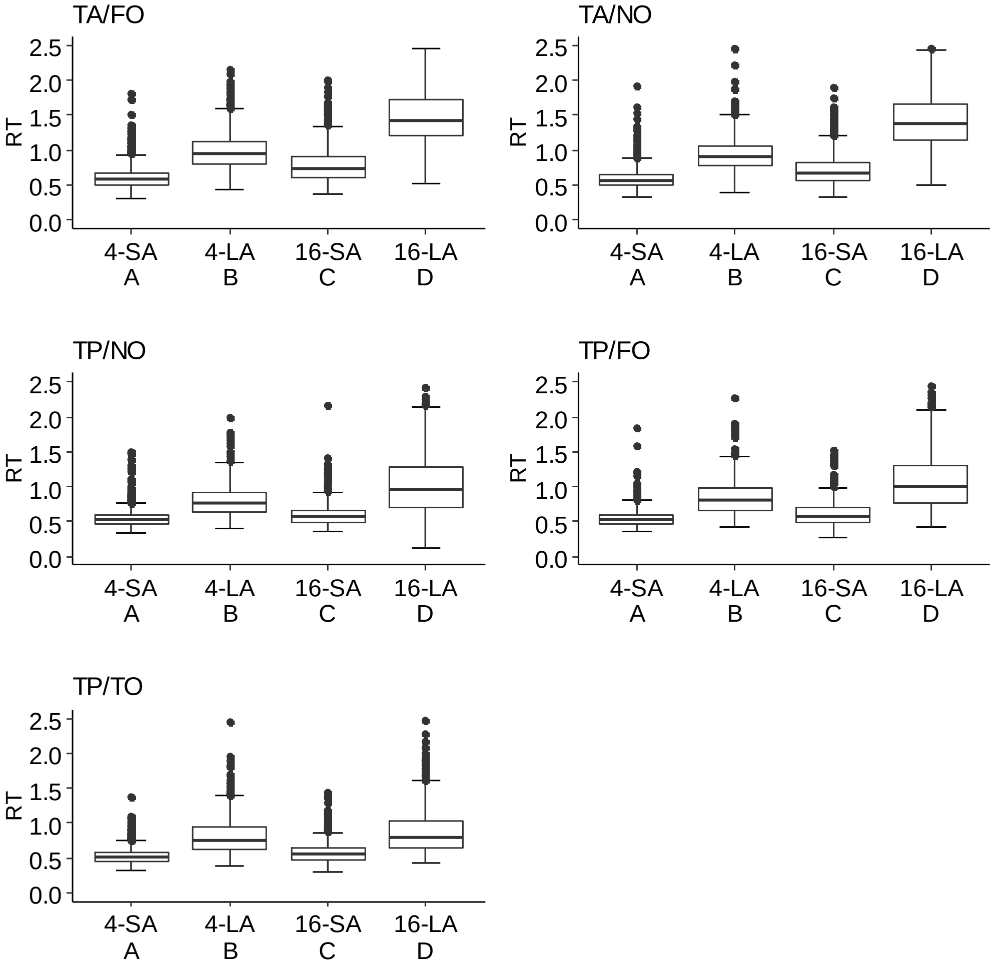

Figure 4.3 The influence of group type (group size and area size) on RT for data subset by dot identity (target status and oddity status). Significant differences between array types, but within subsets, were obtained through glmer analysis (Table 4.2), these are shown below the x-axis using the letters A-D to indicate homogenous subsets, with non-significant differences indicated by a shared letter

*Table 4.2 Pairwise comparisons between different group types, where RT is the response variable and data is subset by dot type. Heavy horizontal lines indicate where models were relevelled to make multiple comparisons between array types. Significance level is indicated by terms in bold, with * for p<0.05, ** for p< 0.01 and *** for p<0.0001***.*

Dot identity	Comparison	Est.	Std. Error	t	p
TA/NO					
	4-SA v 4-LA	0.342	0.008	44.040	**<0.001*** **
	4-SA v 16-SA	0.120	0.006	18.480	**<0.001*** **
	4-SA v 16-LA	0.822	0.011	75.310	**<0.001*** **
	4-LA v 16-SA	-0.222	0.008	-26.870	**<0.001*** **
	4-LA v 16-LA	0.480	0.012	39.900	**<0.001*** **
	16-SA v 16-LA	-0.702	0.011	-62.330	**<0.001*** **
TA/FO					
	4-SA v 4-LA	0.367	0.008	45.750	**<0.001*** **
	4-SA v 16-SA	0.156	0.007	22.950	**<0.001*** **
	4-SA v 16-LA	0.852	0.011	75.690	**<0.001*** **
	4-LA v 16-SA	-0.211	0.009	-24.320	**<0.001*** **
	4-LA v 16-LA	0.485	0.012	38.900	**<0.001*** **
	16-SA v 16-LA	0.696	0.012	59.370	**<0.001*** **
TP/NO					
	4-SA v 4-LA	0.252	0.010	26.395	**<0.001*** **
	4-SA v 16-SA	0.053	0.008	6.698	**<0.001*** **
	4-SA v 16-LA	0.477	0.012	41.249	**<0.001*** **
	4-LA v 16-SA	-0.199	0.010	-20.160	**<0.001*** **
	4-LA v 16-LA	0.226	0.013	17.460	**<0.001*** **
	16-SA v 16-LA	0.424	0.012	35.867	**<0.001*** **
TP/FO					
	4-SA v 4-LA	0.278	0.010	28.363	**<0.001*** **
	4-SA v 16-SA	0.053	0.008	6.692	**<0.001*** **
	4-SA v 16-LA	0.511	0.012	43.047	**<0.001*** **
	4-LA v 16-SA	-0.225	0.010	-22.220	**<0.001*** **
	4-LA v 16-LA	0.233	0.013	17.450	**<0.001*** **
	16-SA v 16-LA	0.457	0.012	37.755	**<0.001*** **
TP/TO					**<0.001*** **
	4-SA v 4-LA	0.266	0.009	29.443	**<0.001*** **
	4-SA v 16-SA	0.040	0.007	5.458	**<0.001*** **
	4-SA v 16-LA	0.333	0.010	34.756	**<0.001*** **
	4-LA v 16-SA	-0.226	0.009	-24.449	**<0.001*** **
	4-LA v 16-LA	0.067	0.011	6.053	**<0.001*** **
	16-SA v 16-LA	0.293	0.010	29.980	**<0.001*** **

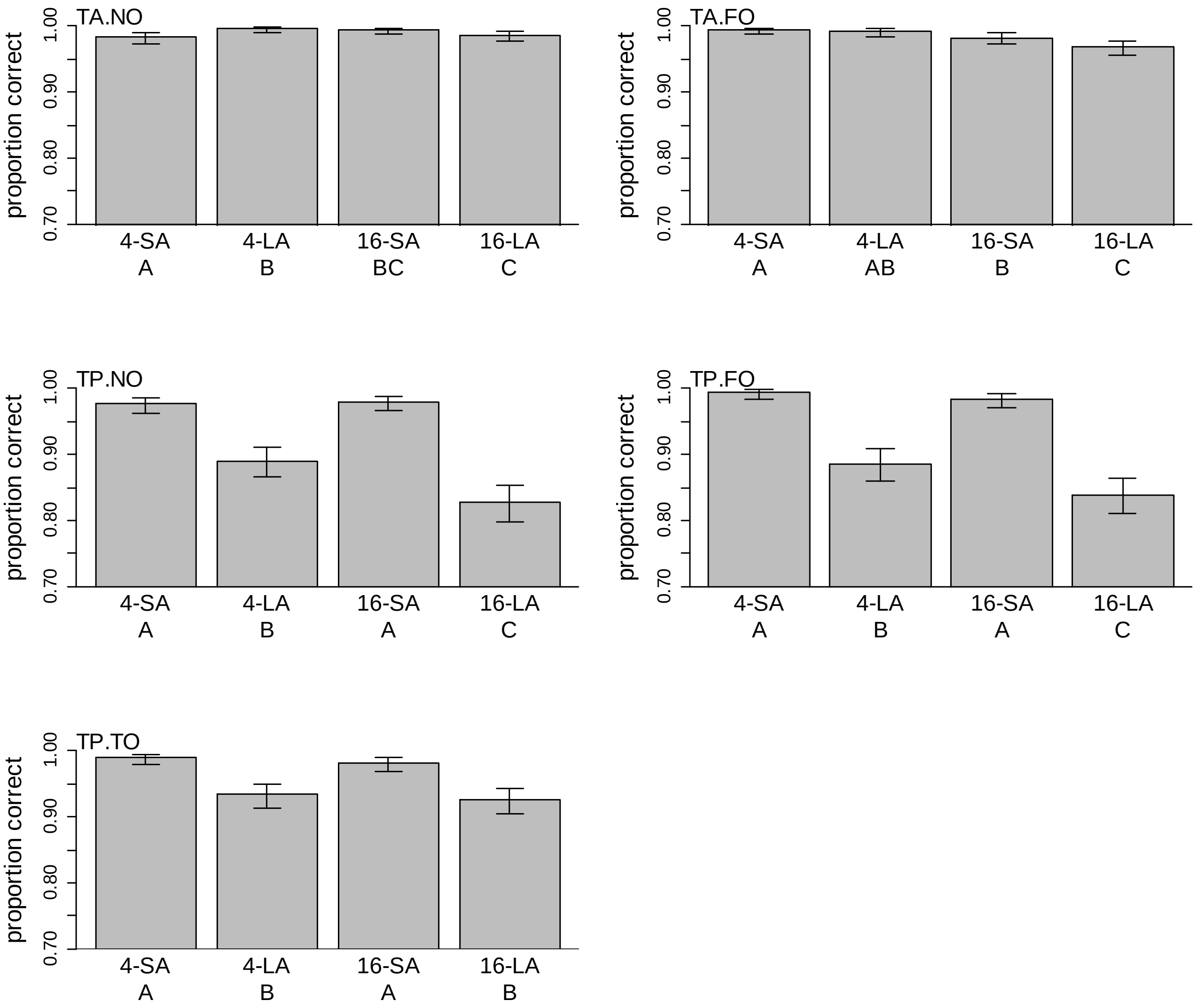

Figure 4.4 The influence of group type (group size and array area) on the proportion of correct responses made by participants. Significant differences between group types, but within subsets, were obtained through glmer analysis (Table 4.3), these are indicated below the x-axis using the letters A-D to show homogenous subsets, with non-significant differences indicated by a shared letter. Error bars represent +/- 2 SE.

*Table 4.3 Pairwise comparisons between different group types, where response accuracy is the response variable and data is subset by dot type. Heavy horizontal lines indicate where models were relevelled to make multiple comparisons between array types. Significance level is indicated by terms in bold, with * for p<0.05, ** for p< 0.01 and *** for p<0.0001***.*

Dot type	Comparison	Est.	Std. Error	z	p
TA/NO					
	4-SA v 4-LA	1.460	0.558	2.618	**0.009****
	4-SA v 16-SA	1.052	0.477	2.207	**0.027***
	4-SA v 16-LA	0.197	0.364	0.542	0.588
	4-LA v 16-SA	-0.407	0.647	-0.63	0.529
	4-LA v 16-LA	-1.262	0.568	-2.221	**0.026***
	16-SA v 16-LA	-0.855	0.490	-1.745	0.081
TA/FO					
	4-SA v 4-LA	-0.291	0.543	-0.535	0.592
	4-SA v 16-SA	-1.116	0.475	-2.353	**0.019***
	4-SA v 16-LA	-1.745	0.447	-3.902	**<0.001*****
	4-LA v 16-SA	-0.826	0.428	-1.928	0.054
	4-LA v 16-LA	-1.454	0.398	-3.656	**<0.001*****
	16-SA v 16-LA	-0.628	0.298	-2.109	**0.035***
TP/NO					
	4-SA v 4-LA	-1.668	0.279	-5.969	**<0.001*****
	4-SA v 16-SA	0.137	0.368	0.373	0.709
	4-SA v 16-LA	-2.210	0.271	-8.152	**<0.001*****
	4-LA v 16-SA	1.805	0.295	6.124	**<0.001*****
	4-LA v 16-LA	-0.543	0.158	-3.426	**<0.001*****
	16-SA v 16-LA	-2.347	0.287	-8.184	**<0.001*****
TP/FO					
	4-SA v 4-LA	-3.139	0.510	-6.152	**<0.001*****
	4-SA v 16-SA	-1.026	0.580	-1.769	0.077
	4-SA v 16-LA	-3.560	0.507	-7.023	**<0.001*****
	4-LA v 16-SA	2.113	0.325	6.511	**<0.001*****
	4-LA v 16-LA	-0.421	0.160	-2.638	**0.008****
	16-SA v 16-LA	-2.534	0.319	-7.940	**<0.001*****
TP/TO					
	4-SA v 4-LA	-1.972	0.403	-4.893	**<0.001*****
	4-SA v 16-SA	-0.550	0.470	-1.170	0.242
	4-SA v 16-LA	-2.086	0.400	-5.210	**<0.001*****
	4-LA v 16-SA	1.421	0.325	4.379	**<0.001*****
	4-LA v 16-LA	-0.115	0.210	-0.545	0.586
	16-SA v 16-LA	-1.536	0.321	-4.778	<0.001*

4.4.2 Q2. How does the presence of *oddity* affect attentional capture, and thus the difficulty or ease of search?

Odd targets attracted attention, resulting in easier search with the shortest RTs, when the target was present and odd (TP/TO) for groups of 16, but not 4 (Figure 4.5, Table 4.4, Table 4.5). RTs for TP/TO were significantly faster than those for any other dot type, in groups of 16 (Figure 4.5, Table 4.4). In groups of 4, there was no significant difference in RT between TP/NO and TP/TO for 4-SA and 4-LA groups, indicating no attention capture by odd targets in smaller groups. However, in groups of 4 (and 16-LA) *oddity* did capture attention when the odd item was a *foil* (TP/FO vs. TP/NO).

Search was most difficult, with the longest RTs, in the presence of an odd foil when the target was both absent and when it was present, again indicating attention capture by oddity (Table 4.5). RT was slower than in homogenous (no oddity, NO) groups, for both TP and TA situations (Figure 4.5, Table 4.4). This was with the exception of 16-SA groups in the TP condition, where there was no significant difference between RTs in the presence of a *foil* and when the group was homogenous (TP/FO vs. TP/NO).

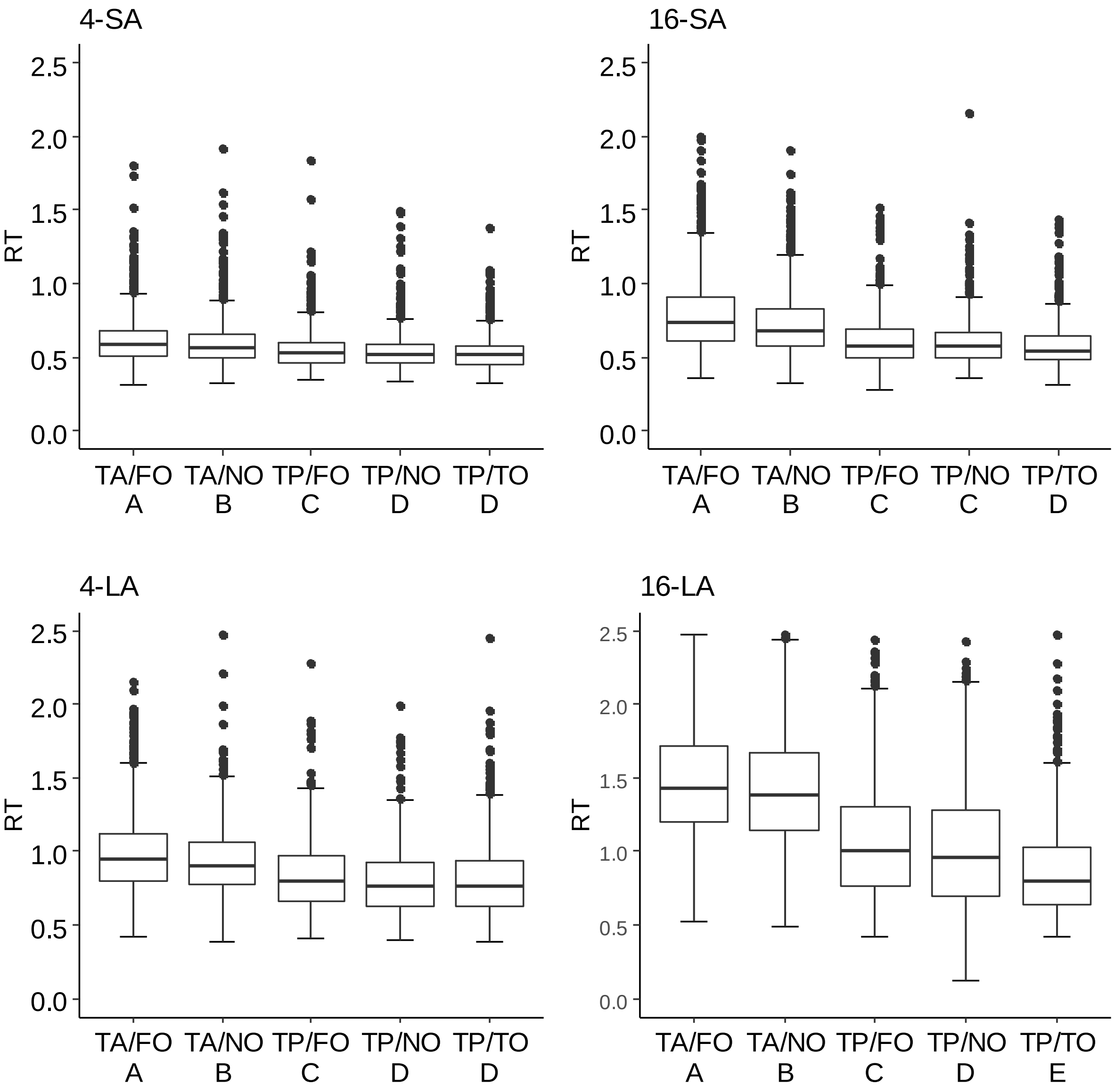

Figure 4.5 The influence of dot identity (target and foil status) on reaction time for data subset by group type (top left of plots). Significant differences between array types, obtained through glmer analysis (Table 4.4), are indicated using homogenous subsets, letters A-E, with non-significant differences indicated by a shared letter.

*Table 4.4 Pairwise comparisons between different dot identities, where RT is the response variable and data is subset by group type. Heavy horizontal lines indicate where models were relevelled to make multiple comparisons between array types. Significance level is indicated by terms in bold, with * for p<0.05, ** for p< 0.01 and *** for p<0.0001***.*

Group type	Comparison	Est.	Std. Error	t	p
4-SA					
	TA/FO v TA/NO	-0.021	0.005	-4.147	**<0.001*** **
	TA/FO v TP/FO	-0.053	0.005	-9.711	**<0.001*** **
	TA/FO v TP/NO	-0.065	0.005	-12.000	**<0.001*** **
	TA/FO v TP/TO	-0.072	0.005	-13.509	**<0.001*** **
	TA/NO v TP/FO	-0.032	0.005	-5.972	**<0.001*** **
	TA/NO v TP/NO	-0.044	0.005	-8.263	**<0.001*** **
	TA/NO v TP/TO	-0.051	0.005	-9.765	**<0.001*** **
	TP/NO v TP/FO	0.012	0.006	2.071	**0.038***
	TP/NO v TP/TO	-0.008	0.006	-1.357	0.175
	TP/FO v TP/TO	0.019	0.006	-3.427	**<0.001*** **
16-SA					
	TA/FO v TA/NO	-0.058	0.007	-7.870	**<0.001*** **
	TA/FO v TP/FO	-0.156	0.007	-20.840	**<0.001*** **
	TA/FO v TP/NO	-0.168	0.007	-22.790	**<0.001*** **
	TA/FO v TP/TO	-0.188	0.007	-25.890	**<0.001*** **
	TA/NO v TP/FO	-0.098	0.007	-13.730	**<0.001*** **
	TA/NO v TP/NO	-0.111	0.007	-15.690	**<0.001*** **
	TA/NO v TP/TO	-0.131	0.007	-18.830	**<0.001*** **
	TP/NO v TP/FO	0.013	0.007	1.779	0.075
	TP/NO v TP/TO	-0.020	0.007	-2.842	**0.004****
	TP/FO v TP/TO	0.033	0.007	-4.621	**<0.001*** **
4-LA					
	TA/FO v TA/NO	-0.046	0.010	-4.609	**<0.001*** **
	TA/FO v TP/FO	-0.142	0.010	-13.512	**<0.001*** **
	TA/FO v TP/NO	-0.183	0.010	-17.980	**<0.001*** **
	TA/FO v TP/TO	-0.175	0.010	-17.098	**<0.001*** **
	TA/NO v TP/FO	-0.096	0.010	-9.342	**<0.001*** **
	TA/NO v TP/NO	-0.137	0.010	-13.817	**<0.001*** **
	TA/NO v TP/TO	-0.129	0.010	-12.926	**<0.001*** **
	TP/NO v TP/FO	0.042	0.010	4.016	**<0.001*** **
	TP/NO v TP/TO	0.008	0.010	0.779	0.436
	TP/FO v TP/TO	-0.034	0.010	-3.234	**<0.001*** **
16-LA					
	TA/FO v TA/NO	-0.051	0.018	-2.780	**0.005****
	TA/FO v TP/FO	-0.393	0.018	-22.150	**<0.001*** **
	TA/FO v TP/NO	-0.441	0.017	-25.390	**<0.001*** **
	TA/FO v TP/TO	-0.580	0.016	-35.290	**<0.001*** **
	TA/NO v TP/FO	-0.342	0.017	-19.740	**<0.001*** **
	TA/NO v TP/NO	-0.390	0.017	-23.020	**<0.001*** **
	TA/NO v TP/TO	-0.529	0.016	-33.080	**<0.001*** **
	TP/NO v TP/FO	0.049	0.016	3.014	**0.003****
	TP/NO v TP/TO	-0.138	0.015	-9.408	**<0.001*** **
	TP/FO v TP/TO	-0.187	0.015	-12.378	**<0.001*** **

Table 4.5 Summary of overall outcomes of the pairwise comparisons illustrated in Table 4.4. For each pairwise comparison, what would be indicated by a significant difference is shown (Sig. indicates). The Outcome column shows the direction of the effect shown in Table 4.4, ↓ indicates a significant decrease in RT, ↑ a significant increase and NS a non-significant difference.

Comparison	Sig. indicates	Outcome	Interpretation
TA/FO v TA/NO	Presence of oddity	↓	Oddity captures attention.
TA/FO v TP/FO	Target presence	↓	Searches take longer when the target is absent.
TA/FO v TP/NO	Target presence and/or oddity	↓	Target presence is important and/or odd target captures attention.
TA/FO v TP/TO	Target presence and/or type of oddity	↓	Target presence is important and/or odd target oddity captures attention.
TA/NO v TP/FO	Target presence and/or presence of oddity	↓	Target presence is more important than oddity (RT for TP is reduced even in the presence of an odd foil).
TA/NO v TP/NO	Target presence	↓	Searches take longer when the target is absent.
TA/NO v TP/TO	Target presence and/or presence of oddity	↓	Target presence is important and/or odd the presence of oddity captures attention
TP/NO v TP/FO	Presence of oddity	**NS** for 16-SA ↑ for 16-LA,4-SA, and 4-LA	In 16-SA groups attention is not captured by an odd foil, target presence is more important that 'distracting' oddity. In all other groups the presence of an odd foil captures attention.
TP/NO v TP/TO	Oddity (type)	↓ for 16-LA and 16-SA **NS** for 4-SA, and 4-LA	Useful oddity is only important in the most challenging group types. In all other groups, additional oddity, beyond target, shape did not decrease RT.
TP/FO v TP/TO	Oddity (type)	↓	Oddity captures attention.

4.4.3 Q3. How does the spatial position of the target in relation to the other items in the array, influence difficulty of search?

For the TP/TO condition search was more difficult, i.e. *RT* was longer, when targets were located on the edge of the group (Figure 4.6a, Table 4.6). However, target nearest neighbour distance only impacted on search difficulty in LA arrays; *RT* was significantly longer the further targets were from their nearest neighbour (Figure 4.6b, Table 4.6).

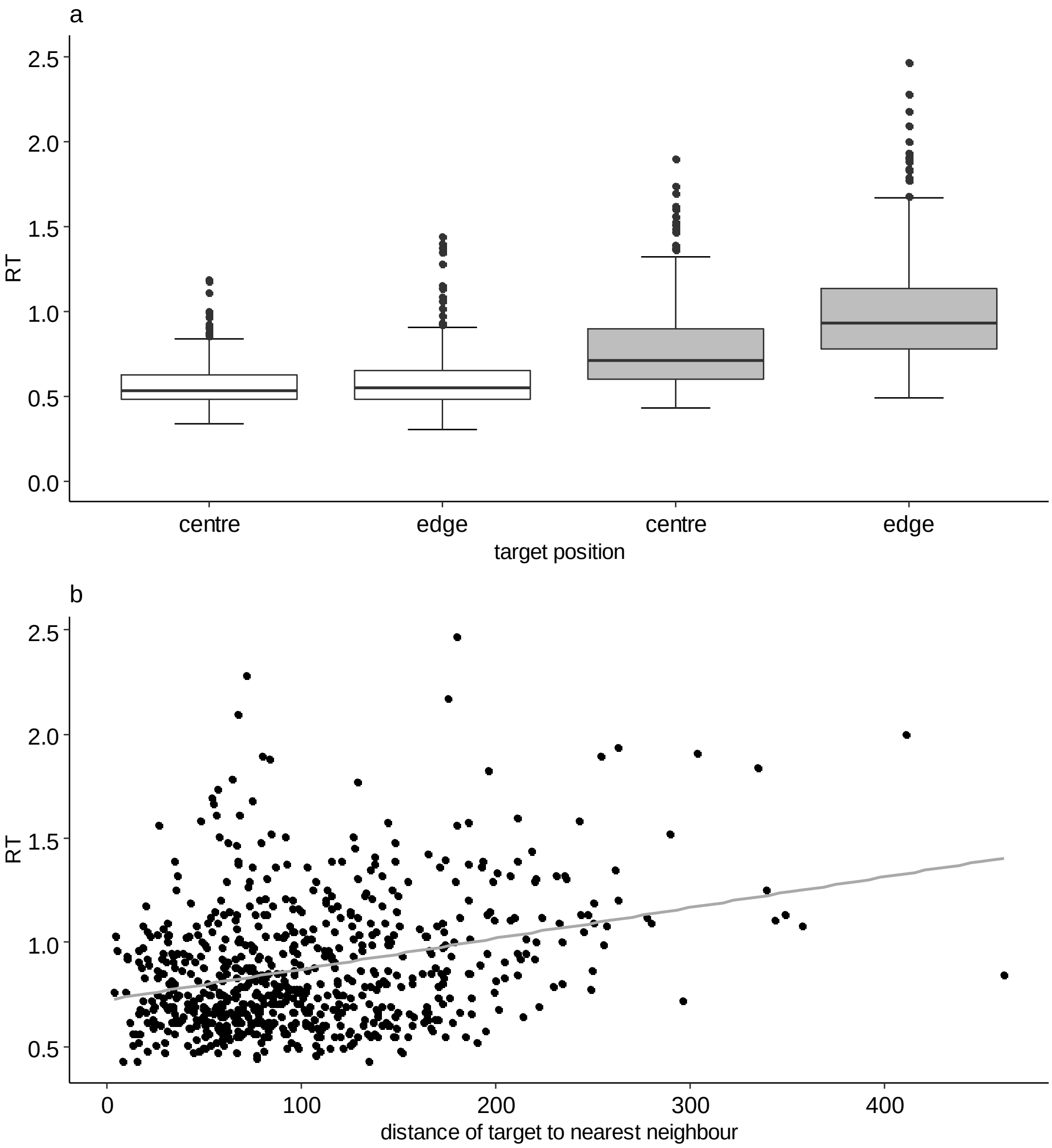

Figure 4.6 a) The influence of target position on RT (secs) in SA (white) and LA (grey) arrays for TP/TO and b) the influence of target distance (pixels) to 1 nearest neighbour on RT (secs) in LA arrays for TP/TO.

*Table 4.6 The effect of spatial variables on RT in the TP/TO condition, for group size of 16 and further subset by array area (small area: SA and large area LA). Significance level is indicated by terms in bold, with * for p<0.05, ** for p< 0.01 and *** for p<0.0001***.*

Variable	**Est.**	**Std. Error**	**t**	**p**
LA				
Intercept	**0.809**	0.029	28.029	**<0.001*** **
Target position	**0.166**	0.021	7.858	**<0.001*** **
Target NN distance	**0.056**	0.011	5.107	**<0.001*** **
SA				
Intercept	**0.574**	0.020	29.364	**<0.001*** **
Target position	**0.028**	0.010	2.920	**0.004** **
Target NN distance	-0.004	0.005	-0.799	0.424

For the TP/NO condition search difficulty was unaffected by spatial variables in SA arrays (Table 4.7). However, for LA arrays, targets took significantly longer to locate when on the edge of the group and when further from their nearest neighbour (Figure 4.7, Table 4.7).

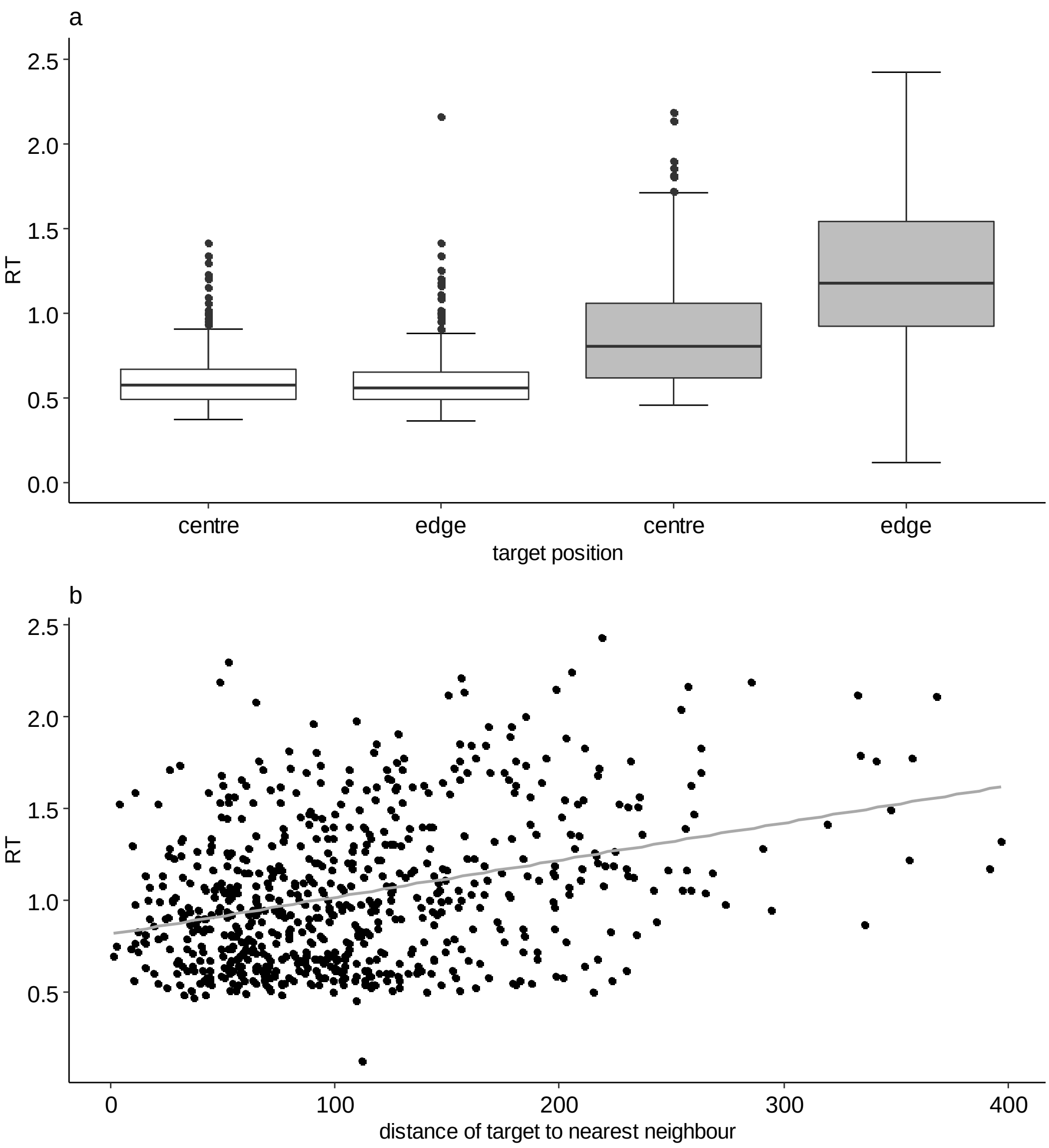

Figure 4.7 a) The influence of target position on RT (secs) in SA (white) and LA (grey) arrays for TP/NO and b) the influence of target distance (pixels) to 1 nearest neighbour on RT (secs) in LA arrays for TP/NO.

*Table 4.7 The effect of spatial variables on RT in the TP/NO condition, for group size of 16 and further subset by array area (small area: SA and large area LA). Significance level is indicated by terms in bold, with * for p<0.05, ** for p< 0.01 and *** for p<0.0001***.*

Variable	**Est.**	**Std. Error**	**t**	**p**
LA				
Intercept	**0.913**	0.037	24.867	**<0.001*** **
Target position	**0.282**	0.030	9.513	**<0.001*** **
Target NN distance	**0.047**	0.015	3.145	**0.002** **
SA				
Intercept	**0.617**	0.025	24.210	**<0.001*** **
Target position	0.000	0.010	-0.006	0.995
Target NN distance	-0.006	0.005	-1.343	0.179

For the TP/FO condition search difficulty was unaffected by spatial variables in SA arrays (Table 4.8). In LA arrays targets took longer to locate when positioned on the edge of the group (Figure 4.8a, Table 4.8). Targets also took longer to locate when further from their nearest neighbour (Figure 4.8b, Table 4.8) and when further from the *foil* (Figure 4.8c, Table 4.8). The position (centre/edge) of the odd dot did not affect RT in SA or LA groups.

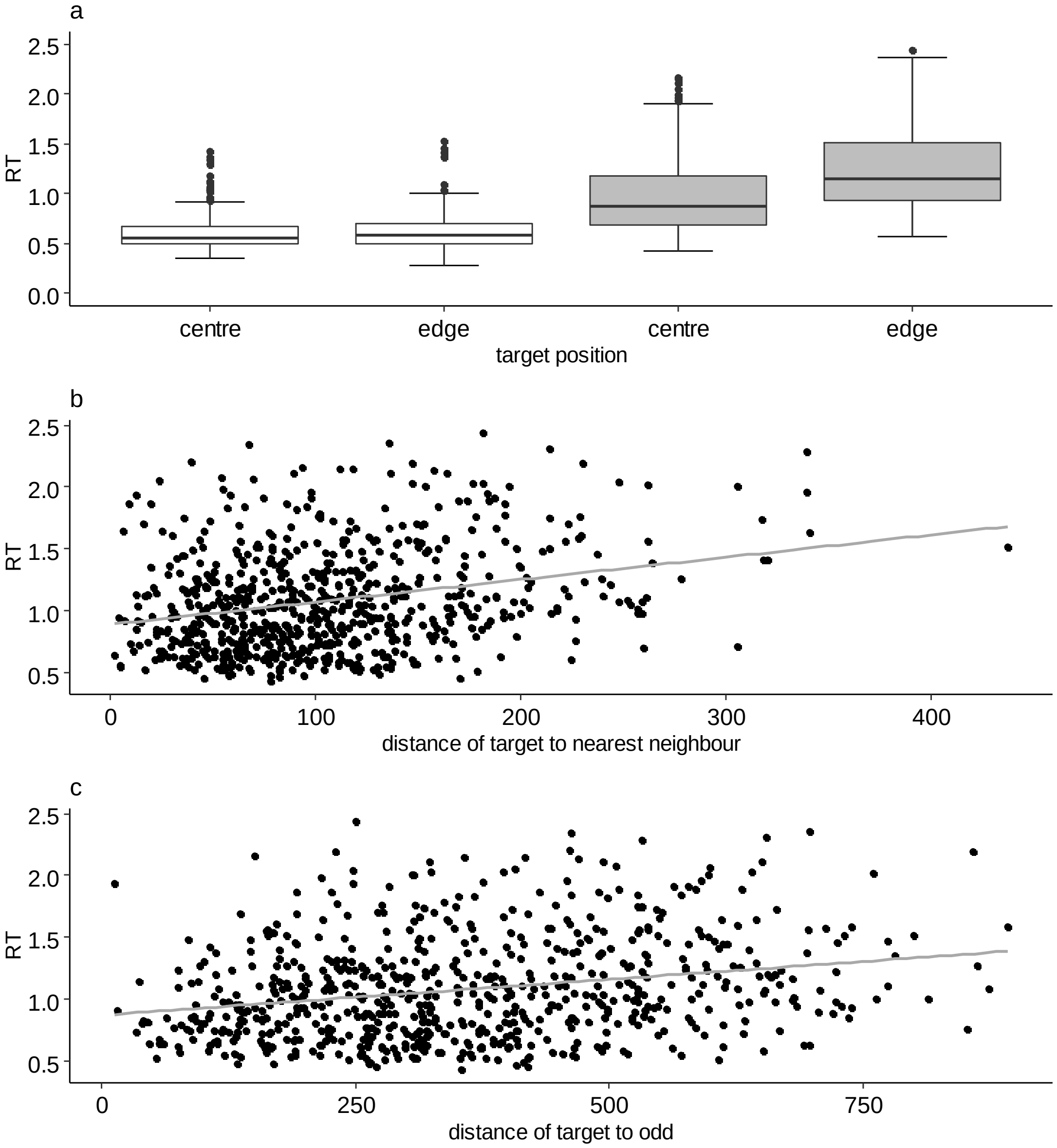

Figure 4.8 a) The influence of target position on RT (secs) in SA (white) and LA (grey) arrays for TP/FO, b) the influence of target distance (pixels) to 1 nearest neighbour on RT (secs) in LA arrays for TP/FO and c) the influence of the target distance (pixels) to the odd foil on RT (secs) in LA arrays for TP/FO.

*Table 4.8 The effect of spatial variables on RT in the TP/FO condition, for group size of 16 and further subset by array area (small area: SA and large area LA). Significance level is indicated by terms in bold, with * for p<0.05, ** for p< 0.01 and *** for p<0.0001***.*

Variable	Est.	Std. Error	t	p
LA				
Intercept	**1.005**	**0.042**	**23.662**	**<0.001*****
Target position	**0.183**	**0.030**	**6.020**	**<0.001*****
Target NN distance	**0.050**	**0.015**	**3.374**	**0.001*****
Odd position	0.011	0.027	0.396	0.692
Odd NN distance	0.007	0.014	0.480	0.631
Target distance to Odd	**0.058**	**0.014**	**4.043**	**<0.001*****
SA				
Intercept	**0.623**	**0.026**	**24.410**	**<0.001*****
Target position	0.016	0.011	1.470	0.141
Target NN distance	-0.006	0.005	-1.166	0.244
Odd position	-0.002	0.010	-0.156	0.876
Odd NN distance	-0.008	0.005	-1.536	0.125
Target distance to Odd	-0.006	0.005	-1.099	0.272

4.5 Discussion

4.5.1 **Q1.** Which combinations of numerical group size and spatial area were most challenging to search?

The difficulty of search and detection was influenced by both group variables (numerical size and spatial area), by dot type (both *target status* and *oddity status*), and by the spatial positions of the target prey-dot and the odd prey-dot within the group.

16-LA were the most challenging groups to search, as evident by searches that took longer and were less accurate. The challenge of larger groups follows through to the attack stage of predation (Ruxton et al., 2007; Hogan et al., 2017b). In humans predating computerised tadpoles, the time taken to successfully capture prey has been shown to increase in response to increased group size (Ruxton et al., 2007). Hogan et al. (2017b) analysed the time taken to make any attack, successful or unsuccessful, in humans targeting computerised starlings within 3-dimensional flocks. Unlike Ruxton et al. (2007) increasing group size decreased attack latency. However, in the same study, numerical group size also reduced attack success. This is suggestive of a trade-off between speed and *accuracy*.

Increasing the size of the area that the participants were required to search was more challenging (LA groups) than increasing the crowding of the prey-dots (SA groups). At the attack stage of predation, the time to successfully capture prey has been shown to be unaffected by group compaction (Tosh et al., 2006b; Ruxton et al., 2007). However, in stickleback predating *Daphnia*, higher local density, which is an artefact of group compaction, increases the spatial error of attacks (Ioannou et al., 2009). In the present study, rather than increasing the challenge of search, a greater degree of prey-dot crowding was advantageous, as all prey-dots were present within the visual field at one time. In LA groups more active searching was required than for SA groups, reducing efficiency and slowing reaction times (Boot et al., 2006). The additional challenge of search in LA groups was not due to increased cognitive requirements. Rather, RTs were longer in response to lower prey densities reducing encounter rate (Stephens & Krebs, 1986).

4.5.2 **Q2.** How does the presence of *oddity* affect attentional capture, and thus the difficulty or ease of search?

The challenge of search associated with the numerically larger group was eased by odd targets capturing attention. Attention capture by salient items (Koch & Ullman, 1987) likely evolved as a mechanism to prioritise behaviourally relevant stimuli, such as immediate threats (Öhman, 1997; Blanchette, 2006) or ripe fruit (Hiramatsu et al., 2008). Our analysis did not aim to directly demonstrate the *pop-out effect* here but rather to look at the sensitivity to *salience* in the context of foraging and predation (*the oddity effect*). While *pop-out* and *oddity* are not, by definition, the same phenomenon, they are similar in that they ameliorate visual '*confusion*' at the detection and attack stages respectively. Pop-out has been demonstrated in a small number of non-human species (zebrafish *Danio rerio*, Proulx et al., 2014; archerfish *Toxotes chatareus*, Ben-Tov et al., 2015; owls *Tyto furcata pratincola*, Orlowski et al., 2015). If tested in a way that met the definitive criteria for *pop-out*, then species subject to the *oddity effect* may also demonstrate the boosted search efficiency that arises from visual *pop-out* (although this is not the case in honeybees *Apis mellifera*, Spaethe et al., 2006). There was no evidence of attention capture by odd targets in groups of 4 (TP/NO v TP/TO).

This suggests that because smaller groups were already sufficiently easy to search, *oddity* was not required for fast detection. It may be that when groups are not confusing the preferential targeting of odd prey does not occur, as other individuals may be equally easy to capture. However, while *oddity* provided no additional predatory benefit in smaller groups, it did affect the difficulty of search when the odd item was a *foil*. Odd *foil*s captured attention in all groups, with the exception of 16-SA, diminishing performance relative to homogenous groups (TP/FO v TP/NO). This finding illustrates automatic, *bottom-up attention capture*, interfering with the pre-defined *top-down* task (Connor et al., 2004) of identifying the presence or absence of the target. This suggests that even if predators do not need *oddity* to overcome *confusion*, odd prey may still be targeted simply because they capture attention. However, in Chapter 3 there was also no preferential targeting of odd prey within smaller groups.

The rapid response times to odd targets and the slower RTs when targets competed for attention with odd *distractors* demonstrate the human visual system's sensitivity to *oddity*. It would be intuitive to think that faster detection would follow through to the next (attack) stage of the predation cycle. However, in non-human animals, faster detection does not necessarily translate to a reduction in attack latency. Kerri tetra (*Inpaichthys kerri)* launched first and second attacks on colour-odd *Daphnia* more often than would be expected by chance. No overall difference between the time taken to attack odd and majority coloured targets was observed (Penry-Williams et al., 2018). While conspicuously odd prey are at increased risk of predation (Ohguchi, 1978; Rodgers et al., 2013; Rodgers et al., 2014) this does not result from decreased time to attack (Penry-Williams et al., 2018). This is suggestive that attacking odd prey is not easier than targeting majority prey. It is possible that odd prey are targeted primarily due to attentional capture and any additional benefits are secondary to that.

4.5.3 **Q3.** How does the spatial position of the target in relation to the other items in the array, influence difficulty of search?

The spatial position of the target affected the difficulty of search in groups of 16 (groups of 4 were omitted from spatial analysis). In LA groups targets took longest to locate when they were spatially isolated (at the edge of the group or further from their nearest neighbour), and when positioned further from an odd *foil*. That proximity to *oddity* affected detection of targets is further evidence that *oddity* draws attention involuntarily.

In animal prey groups attention capture by odd prey may decrease likelihood of attack on prey individuals located further from odd group mates. Landeau & Terborgh (1986) found increased risk to the group as a whole when an odd group member was present, however this does not seem to be reflected by grouping preference. Damselfishes (*Neopomacentrus azysron*, *Chromis viridis* and *Caesio teres*) do not avoid shoaling with a group containing an odd individual in favour of a homogenous group (Quattrini et al., 2018). If odd prey draw attention, then the risk to majority phenotype group-mates will be affected. As far as we are aware, there is no evidence that distance from an odd individual affects risk to majority group individuals. However, theoretically if an individual is further from an odd group member, a predator would have more space to cover in order to launch an attack on distant non-odd members.

Attention capture by *oddity* at the detection stage may also result in odd individuals acting as decoys, allowing other group members to escape while a predator's attention is focused elsewhere (Bateman et al., 2014). This would be dependent on the predator-prey system. For example, a stickleback targeting *Daphnia* can swim faster than their prey and consume multiple *Daphnia* in quick succession (Milinski, 1984). In this case, proximity to *oddity* may be important, but any decoy effect is unlikely. However, a mammal preying on birds would be limited to a single target and the remaining group members could easily escape through flight. Here a decoy effect could be evident but proximity to *oddity* may be unimportant (McQueen et al., 2017). Superb fairy wrens (*Malurus cyaneus*) are less cautious when an odd individual is present within the group, lending support to the decoy hypothesis for this species (McQueen et al., 2017).

Quattrini et al. (2018) demonstrated no avoidance or preference in association at the stage of joining a group in coral reef fish. However, once part of a group, it is unknown whether majority phenotype members interact differently with odd types. In addition to potential aggressive interactions (as discussed in section 3.5) further work could investigate spatial interactions between majority and odd group members. For example, odd individuals could be confined to peripheral positions by majority group mates. Alternatively, odd types may occupy “safer” central positions in an attempt to mitigate the risk of their *oddity* (Morrell & James, 2007; Hirsch & Morrell, 2011; Kimbell & Morrell, 2015a).

In LA groups and 16-SA groups targets positioned on the edge of the group were located more slowly than those in the centre. In contrast, predators attacking prey groups often show a preference for individuals located on the edge of the group, known as marginal predation (Hamilton, 1971). However, the additional “protection” of edge targets observed here can be explained by the same mechanism that explains preferential targeting of edges. Marginal predation is thought to be driven by encounter rate (Duffield & Ioannou, 2017), and here, the central location of the fixation cross (displayed between trials) meant that in contrast to subjects “encountering” edge prey-dots first, centrally located prey-dots would be more “vulnerable”. When considered in this way this result supports that of Duffield and Ioannou (2017).

In LA groups targets were located more slowly when they were a greater distance from their closest neighbours. Higher density regions of groups are more conspicuous, stickleback targeting *Daphnia* will approach these regions more quickly than low density regions (Ioannou et al., 2009). However the spatial error of attacks is increased (Ioannou et al., 2009). Faster decision making is associated with poorer performance in humans (Hogan et al., 2017b). It is possible that a preference for targeting lower density regions in response to confusing group features (Milinski, 1977) is a consequence of a longer processing period leading to a more successful behavioural response. If this is the case, fast decisions in response to attention capture may not lead to the most sensible predatory decisions. However, Landeau and Terborgh (1986) found that attacks by bass towards groups containing odd minnow were both faster and more successful. Penry-Williams et al. (2018) found an association between *oddity* and reduced attack latency, but only in very specific circumstances: for the second attack towards a majority red swarm of *Daphnia* containing one black individual. This effect was absent for attacks towards other odd targets, first attacks and for groups with the inverse colouration. In this chapter the *oddity* of targets conveyed no additional benefit for detection in a numerically small 'easy' prey group. It may be the case that the fish in Penry-Williams et al. (2018) were not sufficiently confused to gain a time advantage from targeting odd prey.

4.5.4 Conclusion

Previous work has demonstrated the association between *oddity* and an increased risk of attack. We suggest that this increased risk begins at the detection stage of predation where *oddity* captures attention over majority group mates. At the detection stage of predation, attentional capture by odd prey can ease the challenge of searching a large prey group. The negative (for the predator) effect of high *local density* on spatial *accuracy* may occur at the attack stage of predation but was not demonstrated here at the detection stage. The presence of *oddity* affects the risk of majority phenotype group members but whether risk is increased (Landeau & Terborgh, 1986) or decreased (McQueen et al., 2017) depends on the predator-prey system in question.

The present findings suggest that proximity to *oddity* may also influence risk to majority type prey and that this warrants further investigation. Further work should take into account both the limitations and capabilities of both predators and prey to make accurate predictions.

Chapter 5. At what point within a mixed group does an odd phenotype attract attention?

5.1 Abstract

Visual predation is constrained by the amount of information that can be processed at one time (the *confusion effect*) therefore, attention must be deployed selectively. The presence of visual distinctiveness, or *oddit*y, within a group of aggregated prey automatically attracts attention, easing the challenge of search. The *oddity effect* can drive both predator selection and prey assortment behaviour. Attention capture by *oddity* at the detection stage of the predation cycle was demonstrated in the previous chapter, indicating that *oddity* functions prior to the attack stage of predation. *Oddity* is a function of group composition. In absence of risk asymmetry, attention capture by a minority phenotype will occur at some point below 50% representation within a group, similarly to the preferential targeting observed in Chapter 2. In this chapter, human predators located visual targets in computerised prey groups in which the prevalence of *oddity* was varied, in order to identify the threshold of attentional capture by a minority phenotype. Results showed that odd prey-dots stopped attracting attention when they made up more than 25% of the group. The mechanisms underpinning the threshold for *oddity* detection remain unknown, however the consequences for prey and overall group risk are discussed. Further work should examine whether *salience* of contrast, capabilities of divided attention, or a combination of these factors underlie the demonstrated threshold. Oddity should also be examined in the context of group conspicuousness and risk to other group members.

5.2 Introduction

Group membership is associated with the dilution of individual risk and other antipredator benefits, such as collective vigilance, communal defence and the *confusion effect* (reviewed in Krause & Ruxton, 2002; see Box 1 for italicised key terms). However, the structure of groups affects the efficacy of these benefits for individual group members. Larger group size dilutes individual risk (Wrona & Dixon, 1991), but less so for prey on the edge of the group compared to their more centrally positioned group-mates (Krause, 1994; Duffield & Ioannou, 2017). The *confusion effect*, where the abilities of a predator to successfully attack a prey group are diminished (Tosh et al., 2006b; Jeschke & Tollrian, 2007), is sensitive to both numerical group size and prey density. As a consequence, larger group sizes and higher local density are both associated with a reduced attack-to-kill ratio (Ruxton et al., 2007; Ioannou et al., 2009). In addition to group structure, predator *confusion* is affected by group composition, for example the behavioural (Ioannou et al., 2012) and phenotypic (Landeau & Terborgh, 1986) similarity of group members enhance the *confusion effect*. At the attack stage of predation success is higher when there is variation in group phenotype (Landeau & Terborgh, 1986).

When a prey group contains two phenotypes, predator *confusion* can be overcome by targeting the minority phenotype, this is known as the *oddity effect* (Mueller, 1971; Ohguchi, 1978). Prey *oddity* is a function of group composition; odd prey are unmatched against the background of their group mates. A conspicuous difference to the rest of the group puts odd members at increased risk of preferential targeting by predators (Almany et al., 2007; Penry-Williams et al., 2018). In addition to this, the presence of *oddity* can increase predator attack success (Landeau & Terborgh, 1986;

Ruxton et al., 2007) and preferential targeting of odd prey, as demonstrated in Chapters 2 and 3, has been linked to increased predator fitness (Rutz, 2012).

Despite the enhancement of predator *confusion* by prey similarity (Landeau & Terborgh, 1986; Krakauer, 1995), and the amelioration of *confusion* by targeting visually distinct prey (Mueller, 1971; Landeau & Terborgh, 1986; Theodorakis, 1989), mixed groups are common (Wolf, 1985; Overholtzer & Motta, 2000; Stensland et al., 2003; Semeniuk & Dill, 2006; Quinn et al., 2012). This can be explained by the complexity of grouping decisions being based on a number of different factors besides *oddity* and *confusion effect*s (e.g. increased forgaging success, reviewed in Krause & Ruxton, 2002). However, the maintenance of mixed groups is possible even in the context of *oddity*, as the benefits of joining an unmatched group outweigh the risk of being a lone individual (Landeau & Terborgh, 1986; Krause & Ruxton, 2002). Oddity also carries different levels of risk for different individuals. Large-bodied stickleback (Peuhkuri, 1998) and *Daphnia magna* (Rodgers et al., 2014) are more at risk of predation when they are odd than smaller group members. For armoured brook stickleback (*Culaea inconstans*), being odd in a group of fathead minnow (*Pimephales promelas*) reduces their risk, as the (unarmoured) minnow are easier to predate (Mathis & Chivers, 2003). In the absence of risk asymmetry odd phenotypes are selected against when they are represented in a small minority (Landeau & Terborgh, 1986; Theodorakis, 1989). In Chapter 3 odd prey were only attacked more than expected by chance when they made up ≤12.5% of the group (≤ 2 out of 16 prey-dots). The generality of this proportion is unknown in both human and non-human predators, and thus any threshold for *oddity* increasing risk is unclear. However, if *oddity* is only costly when an odd phenotype is very rare within a group then a minority phenotype would not be at increased risk provided it exceeded a low threshold.

Attention capture by oddity appears to occur independently of the observer's search goals (Chapter 4), resulting from the higher contrast of odd prey-dots increasing their *salience* relative to the majority phenotype. This type of attentional capture is known as stimulus-driven or *bottom-up* attention (Nothdurft, 1993). For example, a predator approaches a group of prey and a visually distinct group member captures attention over other equally visible group members. In contrast, the deployment of attention, relating to factors internal to the searcher, such as their goals or past experiences, is considered to be *top-down* (Gaspelin & Luck, 2018). For example, a predator approaches a prey group and focuses attention on odd individuals due to the past experience of odd prey being easier to successfully track. *Bottom-up* and *top-down attention*al selection are mechanisms proposed by experimental psychologists (Connor et al., 2004; Gazzaniga & Heatherton, 2006; Theeuwes, 2010), i.e. within a human-centric discipline. However, in principle, these mechanisms could be applied to non-human attentional systems. In Chapter 4 attention capture by *oddity* at the detection stage was demonstrated for human search. It was also evident that proximity to *oddity* has the potential to affect majority type prey. It is unknown how group composition, i.e. the prevalence of a minority phenotype, functions to affect attention capture at the detection stage of predation. In a group made up of two, equally vulnerable and conspicuous phenotypes, it is expected that there should be a threshold, below 50:50, when *oddity* begins to captures attention.

Here, we aim to establish at which frequency within a group odd 'prey' capture the attention of human predators.

We manipulate the frequency of odd items within the ‘prey group’ and explore how *response time (RT)* is affected by *oddity* at different frequencies. As in the preceding chapter, odd items are either the target or a *distractor*, with an odd *distractor* being referred to as a *foil*. Terminology of *dot type* is consistent with the previous chapter (e.g. target present, target odd = TP/TO; target present, no *oddity* = TP/NO). The minority phenotype is referred to throughout by the minority number followed by ‘odd’ (e.g. 1-odd, 2-odd, etc.).

Firstly it is necessary to re-confirm attentional capture by *oddity* (Q1), before moving on to investigate how increasing the prevalence of *oddity* within a group affects attentional capture prior to the attack stage of the predation cycle (Q2, Q3). We therefore ask the following specific research questions with the following predictions:

Q1*. Does oddity capture attention, (does the presence of oddity affect RT?)*

We predict that *oddity* will capture attention, as was the case in the Chapter 4. If attention capture by *oddity* is evident then response time (*RT*) should differ between 0-odd (no odd items) and 1-odd groups. When *oddity* is ‘useful’ to the searcher, i.e. when the target is present and odd (target present, target odd: TP/TO), the presence of *oddity* should make detection of targets quicker, reducing *RT*. Conversely, the presence of *oddity* in groups when the target is absent (target absent: TA) and when the target is not odd but present alongside odd non-targets (target present, *foil* odd: TP/FO) would be distracting. If this is evident, *RT* will be greater in the 1-odd treatment than the 0-odd treatment.

Q2. *Does the effect of attentional capture by oddity diminish with increased prevalence of oddity (does the number of odd prey affect RT?)*

Once attention capture by *oddity* is established, the effect of increasing the prevalence of *oddity* within the group can be investigated. It is predicted that the effect of *oddity* will decline as the number of odd prey-dots (Number Odd) increases, i.e. as the rare prey-dots become less rare. If *oddity* diminishes in importance as it increases in prevalence this would be evident as *RT* increasing beyond 1-odd prey-dot for odd targets (TP/TO). This would be indicated as a significant interaction between TP/TO and Number Odd, with a positive Estimate (Est.) value. For TA and TP/FO groups the same effect may be observed, but with a different direction, i.e. a negative Est. value.

> ***Q3.*** *What is the threshold at which a minority phenotype ceases to capture attention (when does RT for odd targets, TP/TO, increase to relatively the same as for the foil odd, TP/FO, treatment?)*

The threshold at which *oddity* ceases to capture attention can be identified by comparing *RTs* for groups where *oddity* is useful to the searcher (when the target is odd) and when it is not (when *foils* are odd). For example, a significantly faster *RT* for 2-odd in TP/TO vs 2-odd in TP/FO indicates that *oddity* captures attention when there are two odd prey-dots present. When *RTs* for TP/TO are reduced relative to those observed in TP/FO, odd targets no longer capture attention and oddity has ceased being useful to the searcher.

5.3 Methods

The experimental set-up, simulation of prey-dots and experimental procedure were as described in Chapter 4. Unlike Chapter 4, a single group size of 16 prey-dots was presented within a single area. Group composition was varied by changing the number of minority/odd prey-dots present within the group (Number odd, Table 5.1).

As was the case in Chapter 4, participants were required to identify the presence or absence of a moving *target* square prey-dot within a group of circular prey-dots. *Dot type* (the presence/absence of the *target* and the identity of the odd item) varied. When the *target* was present and odd (TP/TO) it was the only odd item in the 1-odd condition. However, from 2-8 odd it was accompanied by other odd (minority coloured) non-target, circular prey-dots. Conversely, when the *target* was not odd (TP/FO) or absent (TA), the relevant number (1-8) of *distractors* were odd.

Participants (n=27) were presented with 432 trials broken down into 3 blocks of 144 to allow for breaks. Prey-dot groups were presented within a 6 x 9 cm area on the screen, with four factors influencing group composition: the number of odd individuals (0-8), the colour of the odd items (dark/light), the identity of the odd item (*target*, *foil* or none/0-odd, and the presence or absence of the *target* (Table 5.2). Participants were asked to identify whether the target (a square prey-dot) was present or absent as rapidly as possible. Participant responses (present/absent) and the time (sec) taken to make the response (*RT*) were recorded for use in analysis.

Table 5.1 the proportion of prey-dot shades within each 'Number Odd' treatment.

Number odd	Group composition (dark:light)
1-odd	1:15 or 15:1
2-odd	2:14 or 14:2
3-odd	3:13 or 13:3
4-odd	4:12 or 12:4
5-odd	5:11 or 11:5
6-odd	6:10 or 10:6
7-odd	7:9 or 9:7
8-odd (mixed)	8:8
0-odd (homogenous)	16:0 or 0:16

Table 5.2 the factors of array appearance and the levels within those factors. Number of repetitions per block of 144 trials are given in parenthesis.

Factor	**Levels**
Odd colour	Dark (72), light (72)
Odd item	Foil (96), target (32), none (16)
Number odd	1-8 (16 for each level)
Target	Absent (72), present (72)

5.3.1 Data analysis

Arrays were coded into 4 categories by the presence/absence of the *target*, and the identity of the odd prey-dot (Table 5.3). *Target* presence is indicated as TP, and *target* absence as TA. In the TP condition, the identity of the odd dot was coded as TO (*target* odd), FO (*foil* odd) and NO (no oddity i.e. the 0-odd condition), giving the 4 *dot-type* categories of TA, TP/TO, TP/FO and TP/NO (Table 5.3). These categories were used in the analysis.

Data were analysed in R v.3.5.0. (R Development Core Team, 2015) using the package lme4 (Bates et al., 2014). Analysis of *RT* was carried out using generalised linear mixed effects models with Gamma errors and an identity link function (Lo & Andrews, 2015). Participant ID was added as a random effect to account for individual differences between participants and multiple responses per participant. As *accuracy* was found to have only minor supplementary value to *RT* data in the previous chapter, it was not analysed here. Instead the analysis focused on the time taken to make an accurate response, incorrect responses were therefore omitted from analysis. A total of 11432 correct responses were obtained from 27 participants, with a mean of 423.41 correct responses per participant. Mean sample sizes for 1-8 odd were 189.93 for TA, 93.10 for TP/FO and 93.30 for TP/TP. For the 0-odd treatments there were a mean of 23.70 correct responses for TA and 23.44 for TP.

5.3.2 Does *oddity* capture attention, i.e. does the presence of *oddity* affect *RT*?

To determine if the presence of *oddity* affected *RT*, pairwise comparisons were made between homogenous (0-odd) and 1-odd groups for each corresponding *group type* (Table 5.3). For the target absent condition, TA 0-odd was compared to TA 1-odd. For the target present condition, TP/NO was compared to the 1-odd data for both TP/FO and TP/TO.

5.3.3 Does the effect of attention capture by *oddity* diminish with increased prevalence of *oddity*, i.e. does the number of odd prey affect *RT*?

To investigate if increasing the number of odd prey affected *RT*, an overall model excluding 0-odd data assessed at the effect of target status (TA, TP/FO and TP/TO) and the number of odd dots (1-8), and their interaction on *RT*.

5.3.4 At what threshold does a minority phenotype cease to capture attention, i.e. when does *RT* for odd targets (TPTO) increase to relatively the same as for the *foil* odd (TPFO) treatment?

To determine a threshold of *oddity*, pairwise comparisons were made between the target present treatments (TP/TO and TP/FO) at each categorical level of 1-8 Number Odd e.g. 1-odd TP/TO vs 1-odd TP/FO; 2-odd TP/TO vs 2-odd TP/FO and so on.

Table 5.3 Target status and the number of repetitions within each experimental block of 144 trials.

Target status	**Identity of odd prey-dot***	**Code used (dot type)**	**Number of times represented per block**
Target Absent	No Oddity (0-odd) Foil Odd (1-8 odd)	TA	72
Target Present	Foil Odd	TP/FO	32
Target Present	Target Odd (1-odd) Target & Foil Odd (1-8 odd)	TP/TO	32
Target Present	No Oddity	TP/NO	8

5.4 Results

5.4.1 Does *oddity* capture attention (does the presence of *oddity* affect *RT*?)

There was a significant difference between the *RTs* for 0-odd and 1-odd in TA and between TP/NO and 1-odd TP/TO groups. The presence of *oddity* increased *RT* for TA groups and decreased *RT* for TP/TO groups, indicating that *oddity* attracted attention, improving search in the TP/TO condition and increasing the difficulty of search in the TA condition (Table 5.4, Figure 5.1). However, for TP/FO groups there was no significant difference in *RTs* between the TP/NO and TP/FO 1-odd groups, indicating that detection of the target was unaffected by the presence of an odd foil (Table 5.4).

Table 5.4 Pairwise comparisons of RT between homogenous groups (0-odd) and 1-odd for each target status. Significance level is indicated by terms in bold, with * for p<0.05, ** for p< 0.01 and *** for p<0.0001***.

Target status	**Est.**	**Std. Error**	**t**	**p**
TA				
	0.035	**0.010**	**3.523**	**< 0.001*** **
TP/FO				
	0.006	0.009	0.669	0.503
TP/TO				
	-0.033	**0.009**	**-3.744**	**< 0.001*** **

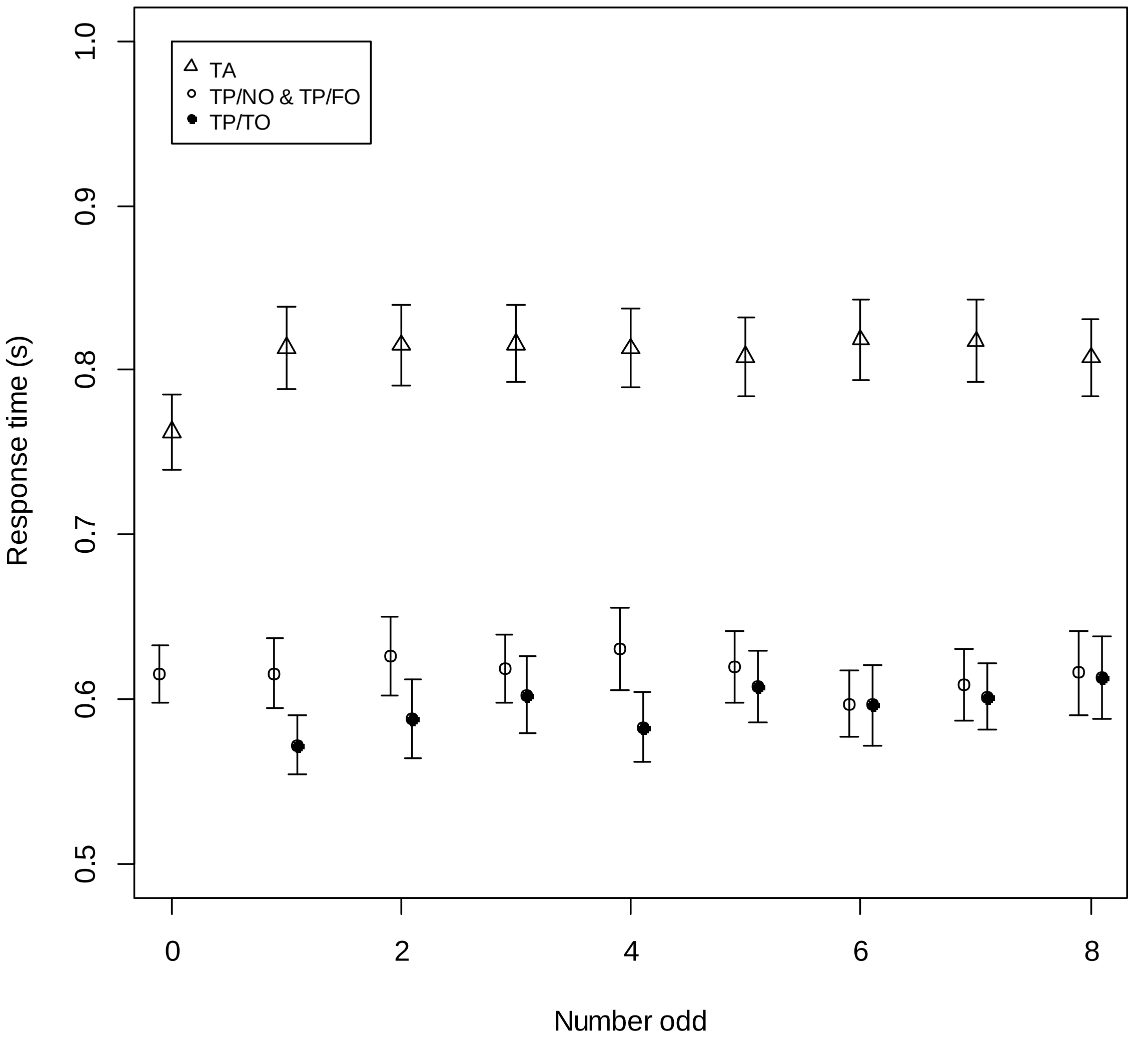

Figure 5.1 Mean RT (+/- @SEM) for the four categories, for the different numbers of odd items in the array. TP/TO has no data for zero odd items because this cannot meaningfully exist, TP/NO is presented using the same symbol as TP/FO to represent zero odd for this category. Sample sizes are balanced across 1-8 odd items, but are larger for the two categories of 0 odd items.

5.4.2 Does the effect of attention capture by *oddity* diminish with increased prevalence of *oddity* (does the number of odd prey affect *RT*?)

The longest *RTs* were observed in TA groups (Figure 5.1), with the presence of the target significantly reducing *RT* (Table 5.5). There was a significant interaction between target status and the number of odd individuals. When the target was absent, increasing the presence of *oddity* beyond 1 odd prey-dot had no further effect and *RT* remained unchanged. Detection of targets in TP/FO groups was also unaffected by increasing the number of odd prey-dots. However, increasing the number of odd individuals affected *RT* for TP/TO: additional *oddity* increased *RT*, indicating the benefit of attention capture by *oddity* reduces as the prevalence of *oddity* increases (Table 5.5).

Table 5.5 RT (sec) as a function of number odd (1-8, treated as continuous data) and target status, and the interaction between these variables. Data for 0-odd is excluded from this analysis. TA is the baseline for this model. Significance level is indicated by terms in bold, with * for p<0.05, ** for p< 0.01 and *** for p<0.0001***.

Variable	Est.	Std. Error	t	p
Intercept	0.812	0.037	22.219	<0.001*
Number odd	0.000	0.001	-0.125	0.901
Target status TPFO	**-0.150**	**0.009**	**-16.811**	**<0.001*** **
Target status TPTO	**-0.195**	**0.009**	**-22.607**	**<0.001*** **
TPFO : Number odd	-0.002	0.002	-0.858	0.391
TPTO : Number odd	**0.004**	**0.002**	**2.299**	**0.022***

5.4.3 At what threshold does a minority phenotype cease to capture attention (when does *RT* for odd targets (TPTO) increase to relatively the same as for the *foil* odd (TPFO) treatment?)

The threshold of *oddity* was identified as ≤4 odd prey-dots. When comparing the target odd and *foil* odd conditions, *RTs* in TP/TO were significantly shorter than those in TP/FO until 5-odd prey-dots were present (Table 5.6). Beyond 4 odd prey-dots, *oddity* no longer captured attention in a way that was ‘useful’ for locating targets quickly.

*Table 5.6 Pairwise comparisons between TP/FO and TP/TO for a given number of odd dots. N = indicates the overall samples sizes for each comparison. Significance level is indicated by terms in bold, with * for p<0.05, ** for p< 0.01 and *** for p<0.0001***.*

Number odd	**Est.**	**Std. Error**	**t**	**p**	**TP/FO N=**	**TP/TO N=**
1	**-0.038**	**0.010**	**-3.948**	**< 0.001*****	314	317
2	**-0.042**	**0.011**	**-4.020**	**< 0.001*****	317	320
3	**-0.022**	**0.011**	**-2.094**	**0.036 ***	311	312
4	**-0.040**	**0.011**	**-3.620**	**< 0.001*****	315	317
5	-0.016	0.011	-1.432	0.152	312	313
6	-0.009	0.010	-0.824	0.410	314	311
7	-0.009	0.010	-0.824	0.410	314	318
8	-0.004	0.012	-0.315	0.753	316	311

5.5 Discussion

Using human predators, we demonstrate that a threshold for *bottom-up* detection of *oddity* exists at approximately 25% of a group of 16 prey-dots. Below this representation, the minority phenotype attracted attention, evidenced by increasing *RTs* as the number of odd dots increased in the TP/TO condition, and reduced *RTs* in the TP/TO condition relative to the TP/FO condition when the number of odd individuals was low. Thus, the minority captured attention when it made up a low proportion of the group, but this effect was reduced as the minority phenotype became more common. Further evidence that odd individuals capture attention is shown in the TA condition, where the presence of any number of odd prey-dots increases *RT* relative to no odd dots, and in the TP/TO condition, where the fastest reaction times are seen when there is a single odd prey-dot, which is also the target.

In contrast to Chapter 4, *oddity* did not appear to capture attention in the TP/FO condition. There was no difference in *RT* between 0-odd and 1-odd when the odd item was a *foil* and the target was present, contrasting with our expectation that the presence of *oddity* would increase *RT* due to attention being drawn away from the target. Salient items typically draw attention because they contrast with their surroundings (Bundesen, 1990; Bundesen et al., 2015). This was evident when the task-relevant target was absent (TA prey-dot groups), but not when it was present, but not odd (TP/NO). An additional factor that can contribute to *salience* is goal relevance (Bundesen, 1990, Nordfang et al., 2013). One possibility is that goal relevance (feature relevance; Bundesen et al., 2015) was also incorporated into the 'map' (Wolfe, 1994; Desimone & Duncan, 1995; see Box 1 for saliency maps) that guided the attention of participants in a *bottom-up* manner (Navalpakkam & Itti, 2005; Tanner & Itti, 2019). Thus, in the TP/NO condition, the *oddity* of the target (a square) relative to the *distractors* (circles) may have been sufficient to capture attention in this condition, and the cumulative *oddity* (or additive salience; Nothdurft, 2000) of shape and luminance reduced *RT* to the fastest observed between *group type*s in the TP/TO condition.

In Chapter 3, a threshold for *oddity effect* was also demonstrated at the attack stage of predation. Fish preferentially targeted odd prey-dots when they made up only ≤ 2 of the 16 dots. Here, the threshold of *oddity* observed in TP/TO groups was 4 out of the 16 dots, but similarly to Chapter 3, it is not possible to state whether this is an absolute value or a proportion of the group. Two possible explanations for this threshold are proposed: sufficient contrast for *salience* and the ability to track multiple objects. Beyond 4 individuals, 25% of the group, odd prey-dots may no longer contrast against the majority prey-dots sufficiently enough to elicit an effect of increased *salience* (*feature contrast*; Bundesen et al., 2015). If this is the case, then the threshold should be maintained at 25% when the size of the group is increased. Alternatively, humans can use divided attention to track multiple objects (*multiple object tracking, or MOT*; Pylyshyn & Storm, 1988) to the same threshold observed here for *oddity*: *MOT* indicates that around 4 different objects can be tracked simultaneously. The ability of non-humans to divide attention between multiple moving targets has not been studied as explicitly as *MOT* but divided attention in search has (Dukas & Kamil, 2000; 2001; Dukas, 2002a). The *confusion effect* could be considered to arise from an inability to successfully divide attention between multiple, moving targets within a prey group (Krakauer, 1995). The threshold of *MOT* can vary with task complexity, with increasing complexity decreasing the number of items that can be tracked simultaneously (Alvarez & Franconeri, 2007). Increasing the number of items within an array would typically increase the difficulty of a task and reduce the *MOT* threshold. However, *oddity* has been shown to ease the difficulty of search in both the present and previous chapters and may therefore mitigate this effect, aiding tracking ability through distinctiveness of target items. It may be the case that focusing on odd prey – a conspicuous minority – eases the burden of dividing attention between multiple potential targets.

Dividing attention between two types of cryptic prey reduces the ability of trained blue jays to successfully detect computerised moths (Dukas & Kamil, 2000; 2001; Dukas, 2002a). Focusing attention on search for one specific prey type (search image, Tinbergen, 1960; Pietrewicz, 1977) is a way to reduce the effect of divided attention. Search image formation results in focus on a common prey type, while ignoring other prey types (Dukas & Kamil, 2000; Punzalan et al., 2005). Preferentially targeting the most common phenotype is contrary to the predictions of the *oddity effect*, where rare prey are selected (Ohguchi, 1978). Search image and *oddity* may function under different attentional mechanisms to overcome the same problem of reduced attack rate. In terms of attentional strategy, search image would be considered top-down, while the selection of odd prey may result from *bottom-up* attention capture. When prey is cryptic the visual system is not confused by multiple prey, but a focused *top-down* strategy is required in order to detect prey. When prey are present within a confusing group, detection is not an issue, whereas identifying which prey to target may be. Oddity could function *pre-attentively* to select a target in *bottom-up* manner, without creating any additional cognitive burden.

In an ecological context, the results of this chapter suggest that prey groups may benefit from being joined by unmatched individuals, if they raise the representation of the minority phenotype above the threshold of *oddity*. When presented with a choice between entirely matched and entirely unmatched groups, individuals demonstrate a preference for matched groups (Rosenthal & Ryan, 2005; Rodgers et al., 2010). For example, rainbow fish (*Melanotaenia australis*, Rodgers et al., 2010) and mollies (*Poecilia sphenops*, Rodgers et al., 2013) preferentially group with colour matched shoals. Exceptions to avoiding *oddity* within mixed groups occur when there is asymmetry of risk, for example where one species is more difficult detect (Rodgers et al., 2013) or consume (Mathis & Chivers, 2003). The findings of this chapter, and those of Chapter 2, suggest that where no such asymmetry is present, a partially unmatched group should be preferred over an entirely unmatched group. Through increasing the representation of a minority phenotype above a threshold, *oddity* ceases to a) capture attention (this chapter) and b) be preferentially targeted (Chapter 2).

Because conspicuously odd individuals capture attention it is intuitive to think that the presence of *oddity* therefore increases the overall conspicuousness of a prey group. If this were the case then the findings of this chapter suggest that all group members, not just the minority phenotype, would benefit from additional minority phenotype individuals joining a group. However, detection may not translate into increased risk of attack to majority type group members. From the perspective of a predator, there has been no explicit testing of whether groups containing odd individuals are more conspicuous. However, groups of ten *Daphnia* containing two odd individuals are attacked first more often than uniform groups by stickleback predators (Ohguchi, 1978). On the contrary, the grouping preferences of three species of reef fish (*Neopomacentrus azysron*, *Chromis viridis* and *Caesio teres*) show no indication that groups containing an odd individual have greater overall risk than uniform groups (Quattrini et al., 2018). If groups are more detectable when they contain odd individuals, the risk of attack to majority types may still be reduced as a consequence of odd prey being preferentially targeted. Evidence that the presence of an odd group mate is advantageous is seen in superb fairy-wrens (*Malurus cyaneus*). Brown coloured fairy-wrens (females and pre-moult males) exposed to alarm call playback will return to open areas more quickly when one or two odd blue males are present within the group (McQueen et al., 2017). It is possible that odd males act as a decoy, capturing the attention of the predator while majority type group mates are able to escape (McQueen et al., 2017), thus all individuals would benefit from an odd member joining. An instance where attentional capture by a conspicuously odd individual could be costly for more vulnerable group members is where asymmetry of risk is present within a group. For example, detection of conspicuously coloured male guppies may lead to preferential targeting of their less conspicuous, but larger and therefore more profitable, female groupmates (Pocklington & Dill, 1995).

The conspicuousness of groups to predators is also affected by the overall group structure (Uetz & Hieber, 1994; Ioannou & Krause, 2008). When using approach time as a proxy for conspicuousness, factors such as group size appear to increase the detectability of groups (Uetz & Hieber, 1994). For example, stickleback will approach groups of *Daphnia* more quickly when the groups are larger (Ioannou & Krause, 2008) and denser (Ioannou et al., 2009). The greater conspicuousness of larger prey groups may interact with the composition of the group to affect which individuals are targeted. For example, in a smaller group attention may be captured by an odd individual but attacks may be directed towards a more profitable individual. In a larger group, odd individuals may both be detected and attacked in response to the higher contrast of *oddity* and predator *confusion* elicited by group size. Studies that examined any cumulative conspicuousness of group structure and composition would need to take into account that encounter rate for finite prey populations decrease with increasing group size (Ioannou et al., 2011).

In some instances, higher *salience* of a group member compared to their group mates can be beneficial. In lekking bird species, female choice of mate is based on a number of traits (Höglund & Lundberg, 1987; Petrie & Halliday, 1994; Lanctot et al., 1998; Shorey, 2002) but the colour and conspicuousness of plumage often ranks as a highly important factor (great snipe, *Gallinago media*: Höglund et al., 1990; golden collared manakin *Manacus vitellinus*: Stein & Uy, 2005; peacock *Pavo cristatus*: Loyau et al., 2007). Plumage brightness is positively associated with mating success in golden collared manakins (Stein & Uy, 2005), as is eyespot iridescence in peacocks (Loyau et al., 2007). Some lekking species (e.g. Marine iguanas, *Amblyrhynchus cristatus*: Wikelski et al., 1996; little bustard, *Tetrax tetrax*: Jiguet & Bretagnolle, 2006) may attempt to benefit from positioning themselves near to an attractive, attention-grabbing ‘hotshot’ male (Beehler & Foster, 1988) that draws females to the area. There can be a trade-off between showing off to potential mates and capturing the attention of potential predators (Pocklington & Dill, 1995; McQueen et al., 2017). Therefore an ideal strategy is to exploit the visual sensitivities of the intended audience, such as potential tetrachromat mates, while not appearing conspicuous in the visual system of a dichromat mammalian predator, for example (Kane et al., 2019). The present study used contrast *oddity* based on differences between light and dark stimuli. Because of this, the results are more widely applicable across visual systems, and therefore species, than if stimuli contrasted chromatically, i.e. they were colour-odd (Land & Nilsson, 2012).

This chapter demonstrates a threshold for the detection of *oddity*. However whether *salience* due to contrast, capabilities of divided attention, or a combination of these factors underpins this threshold is unknown and requires further study. In an ecological context, minority phenotype group members benefit from increased representation within a group. This benefit may extend to majority type group members and further work should focus on whether the presence of odd individuals affects overall group detection, and how this interacts with group structure to affect risk to different group members.

Chapter 6. General discussion

6.1 Summary in brief

The broad aim of this thesis was to apply principles from psychology to the study of the *oddity effect*. In Chapter 2, it was established that computerised stimuli, commonly used in psychology to examine human perception, were a viable and practical method for studying *oddity effect*s (as defined by the preferential targeting of odd prey) in a naive non-human predator (aim 1). Chapter 3 went on to empirically demonstrate that odd targets are at increased risk of preferential targeting within larger groups relative to smaller ones (aim 3). Numerical group size, rather than area or density, was identified as driving the selection of odd prey. The increased 'importance' of *oddity* in larger prey groups was further demonstrated at the detection stage with human 'predators' in Chapter 4. Here, *oddity* attracted attention, diminishing the challenge of searching larger groups (aim 4). Results also suggested that the risk of majority type group members was influenced by their proximity to odd group-mates. In Chapter 5 it was established that odd prey-dots stopped attracting the attention of human participants when they made up more than 25% of the group (aim 5). A lower threshold (12.5%) was observed for the preferential targeting of odd prey by fish predators (aim 2; Chapter 2). In Chapter 3, fish were least likely to attack numerically large, but dense (16-SA) groups, indicating that there is a limit to the 'usefulness' of *oddity* for fish predators.

6.2 Using principles from psychology to understand an ecological question

The *pop-out effect* in psychology is characterised by the independence of time taken to locate a unique target to the number of items with a scene or array (Ben-Tov et al., 2015). When an odd target can be detected equally as fast between a small and large group, the definitive criteria for *pop-out* is met (Wolfe, 2016). The *oddity effect* also occurs in response to the presence of a visually distinct minority within a group of majority type items, or prey (Landeau & Terborgh, 1986; Theodorakis, 1989; Penry-Williams et al., 2018). However, the *oddity effect* as a concept is more broadly defined as relating to the risk of odd prey and the ability of predators to launch successful attacks on prey groups. Oddity is typically (but not always, Almany & Webster, 2004) examined in conjunction with predator *confusion*, as a means to ameliorate the challenge of preying on confusing groups (Landeau & Terborgh, 1986; Ruxton et al., 2007; Penry-Williams et al., 2018). The *pop-out effect*, however, pertains specifically to attentional capture, meaning the two terms are not interchangeable.

This is the first study to look at the *oddity effect* using a non-human predator targeting a computerised prey group. Prior to this, studies into the *oddity effect* have artificially manipulated phenotype (Ohguchi, 1978; Landeau & Terborgh, 1986; Rodgers et al., 2013) or used colour morphs of the same species (Mueller, 1971; Rodgers et al., 2013). Chapter 2 outlined how the use of computerised 'prey' can improve the study of *oddity* across three areas: control, ethics and efficiency. The highly controllable nature of computerised stimuli minimises confounding factors, such as colour morphs of the same species also exhibiting different behavioural phenotypes (Horth, 2003, Hetem et al., 2009, Dijkstra et al., 2017). Ethical practice is improved through a reduction in the use of live animals (Behaviour, 2012), particularly in relation to phenotypic manipulation, or actual predation. Efficiency is enhanced as a result of being able to reuse and share code, and experimental productivity can be improved through running code as opposed to 'preparing' live prey.

Within this thesis, different approaches and tasks were employed for humans (detecting a pre-assigned *target* amongst prey-dots, Chapters 3 and 4) and fish (attacking any prey-dot, Chapters 1 and 2). For examining attentional capture in human subjects a task involving a pre-determined *target* is necessary (Bundesen and Habekost, 2008). Non-humans cannot be directly communicated with to explain a task, consequently experimental procedures must be based on naturally occurring behaviours (Ohguchi, 1978), often coinciding with some training (Rischawy & Schuster, 2013; Orlowski et al., 2015). Therefore, human subjects were used to examine attentional capture by *oddity* and fish were used to examine the preferential targeting, or choice, of odd targets, using these different, but subject-appropriate techniques.

These different approaches reflect the fact that *oddity effect*s can potentially operate at two different stages of the predation cycle. Initially, *oddity* attracts the attention of potential predators (as shown in Chapters 4 and 5), and subsequently odd individuals may be preferentially targeted (Chapters 2 and 3). However, it is not known, from the literature or the findings of this thesis, whether preferential targeting occurs due to *oddity* attracting the attention of fish (i.e. *bottom-up* attention capture), or whether predators strategically choose to target odd prey, potentially to overcome *confusion effect*s. It is possible that all these explanations are true: odd prey could be targeted for either reason, and this thesis has shown that both potentially operate. Future work could focus on disentangling these two components of *oddity*.

6.3 When is oddity important?

In Chapters 4 and 5 *oddity* captured attention for human predators, as demonstrated by faster detection of odd targets relative to targets that were not odd. In Chapters 2 and 3, it was not explicitly demonstrated that fish predators were choosing odd targets due to attention capture, however attentional capture by higher *saliency* is implied by preferential targeting (Ben-Tov et al., 2015). Attentional capture by odd items has been demonstrated elsewhere in non-human animals through the study of the *pop-out effect*. Archerfish will preferentially target odd targets, similar to the findings in Chapters 2 and 3 of this thesis (orientation oddity, Mokeichev et al., 2010; speed oddity and orientation oddity, Ben-Tov et al., 2015). Attentional capture of odd targets is demonstrated by an independence of archerfish *RT* to the number of *distractor* items present (Ben-Tov et al., 2015). Pop-out for orientation *oddity* has also been demonstrated in owls (Orlowski et al., 2015), where the number of saccades before fixating on odd targets, and the time taken to do so (fixation time, a more owl appropriate version of *RT*), were independent of the number of *distractors* present. Through the psychologically defined measures of attention capture, *oddity* does attract attention, and this appears to occur in a similar way in both human and non-human animals.

For both fish (Chapter 3) and humans (Chapter 4) *oddity* was most important when presented with groups that were potentially more challenging to search or attack, specifically those that were numerically large. In smaller groups oddity was not required for fast detection of prey-dots (humans), nor were odd prey-dots preferentially targeted (fish). This is the first study to empirically demonstrate that odd prey are at increased risk of preferential targeting in larger prey groups (Chapter 3). Other studies examining the preferential targeting of odd prey have used a single group size (10 mice: Mueller, 1971; 10 *Daphnia*: Ohguchi, 1978; 1 *Daphnia* Rodgers et al., 2013; 12 *Daphnia*: Rodgers et al.; 2015, 10 *Daphnia*: Penry-Williams et al.; 2018, 11 *Daphnia*: Raveh et al., 2019, 30 minnow: Theodorakis, 1989) with the exception of

Landeau and Terborgh (8 and 15 minnow, 1986), who did not demonstrate any effect of *oddity* in larger groups. For humans targeting computerised prey, odd targets were captured more quickly than majority type, and this was independent of group size (Ruxton et al., 2007).

The increased vulnerability by odd targets in larger groups is supported by predictions made using artificial neural network models (Krakauer, 1995). "Predator" *accuracy*, modelled by an algorithm, was improved on odd targets. Furthermore, in 2 out of 3 of the programmed wiring schemes, the vulnerability of odd targets was increased in groups of 4 versus groups of 2. An explanation for increased preferential targeting in larger groups is that an odd target has greater contrast, and therefore *salience* (Nothdurft, 2006; Pike, 2018), when situated with a greater number of dissimilar individuals. The increased *salience* of the odd individual follows through to the attack stage of predation, increasing preferential targeting of odd prey in larger groups.

Oddity is often discussed as a mechanism by which predators can manage the behavioural consequences of the *confusion effect* (Landeau & Terborgh, 1986; Penry-Williams et al., 2018). These consequences include an unwillingness to target confusing groups and high attack latency when faced with confusing groups (Milinski, 1977; Schradin, 2000). By this definition, fish appeared to be most confused by numerically large and dense groups (16-SA; Chapter 3), which they were most likely to refuse to attack within the allotted time. For fish targeting numerically large groups (16-SA and 16-LA), targeted prey-dots were more likely to be odd, but *oddity* did not appear to help overcome the *confusion* elicited by 16-SA groups. The presence of *oddity* has previously been shown not to decrease the attack latency of stickleback preying on *Daphnia* (Penry-Williams, 2018). In addition, when attacks are launched, the presence of *oddity* cannot always ameliorate *confusion effect*s (Landeau and Terborgh, 1986). Bass preying on groups of 8 were able to attack and kill minnow. However when the group size was increased to 15, 194 unsuccessful attacks were launched – a 0% success rate, despite the presence of odd minnow within the group (Landeau and Terborgh, 1986).

The spatial area of prey groups, i.e. whether groups were dispersed over a large area (LA) vs. confined to a small area (SA), did affect the detection of targets (humans, Chapter 4) but did not affect the preferential targeting of odd prey (fish, Chapter 3). Fish did have a higher occurrence of refusal to attack 16-SA groups, however, the targeting of odd prey was not increased relative to 16-LA groups. Humans found numerically large, but spread out, groups most challenging, as evident by the longest *RTs* (Chapter 4). Unlike fish presented with 16-SA groups, humans were able to use *oddity* at the detection stage to overcome the *confusion* associated with searching a challenging prey group. The different stages of predation associated with the human (Chapter 4) and fish (Chapter 3) experiments explains why large-area groups were most challenging for humans while small-area groups were most challenging for fish. At the detection stage, when searching for a pre-defined *target*, a larger search area with more dispersed prey-dots reduced encounter rate (Turesson & Bronmark, 2007) with the *target* for humans, increasing *RT*. At the attack stage of predation, fish that were faced with a small-area group were potentially overwhelmed by the high local density of potential targets (Ioannou et al., 2009), and better able to target prey in more dispersed groups.

6.4 The threshold of oddity

A potential threshold of *oddity* was indicated for both fish (Chapter 2) and humans (Chapter 5), although this threshold was numerically different between chapters. In Chapter 2, odd prey-dots were preferentially targeted by fish below 12.5% of group representation (2 out of 16 dots). In Chapter 5, odd prey-dots attracted attention below 25% of group representation (4 out of 16 dots). However, since only one group size was assessed in these chapters, it is not possible to determine whether this threshold is an absolute number or a proportion of the available prey-dots, and further work is needed to determine this.

The thresholds of *oddity* could rely on the ability to simultaneously track multiple objects (*multiple object tracking, MOT:* Pylyshyn & Storm, 1988). For human detectors, attention was captured by odd *targets* when there more no more than 4 odd prey-dots, this is the same as the generally accepted threshold for *MOT* (Doran & Hoffman, 2010). In order to locate the target amongst the odd prey-dots, attention may have been divided to simultaneously track which odd items had already been inspected (Doran and Hoffman, 2010). The divided attention capabilities of humans and fish are both subject to the complexity of a task. For example, in humans, fewer fast moving stimuli can be tracked simultaneously than is possible for slow moving stimuli (Alvarez & Franconeri, 2007). We do not know whether there is a threshold of *MOT* in fish. However when guppies (Godin and Smith, 1988) maintain a higher feeding rate on large *Daphnia* groups, the probability of their capture by a cichlid predator increases, relative to feeding at a lower rate on smaller prey groups. Group composition can also have consequences for attentional allocation (Griffiths et al., 2004). Trout associating with unfamiliar conspecifics must allocate a certain amount of attentional resources to aggressive within-group interactions (Griffiths et al., 2004). Through associating with familiar conspecifics, trout are able to divide their attention between fewer tasks, allocating more time to foraging while still responding 14% more quickly to the presence of a predator (Griffiths et al., 2004).

The difference between fish and human subjects in the thresholds of *oddity* may be a consequence of the different stages of predation, or related to their capabilities of tracking objects. It is also possible that the different environments that fish and humans inhabit affect the thresholds of attentional capture by stimuli. Light in aquatic environments is more scattered than light in terrestrial environments (Land & Nilsson, 2012). Scatter reduces the amount of light coming from an object, reducing contrast (Johnsen, 2012). Sufficient contrast with surrounding prey-dots would be necessary for odd prey-dots to be *salient* (Bundesen, 1990; Bundesen et al., 2015). It may be that for fish subjects, the threshold of *oddity* was lower because contrast (between odd items and the background of the group) needed to be higher to account for light scatter. Further investigation is required to ascertain which factors underpin the different thresholds observed, and whether the indicated thresholds are absolute or proportional. For example, for stickleback, are odd prey targeted when there are no more than a total of 2 odd individuals, or when these individuals make up no more than 12.5% of the group?

6.5 Spatial position and target choice

In Chapters 4 and 2, the spatial position of targets influenced their detection by humans and selection by fish, respectively. Spatially isolated targets were harder to find (Chapter 4), but spatially isolated prey-dots are were more likely to be targeted (Chapter 2). This initially seems like a contradiction, however human subjects started their search from a centrally located fixation point. The increase in detection time for edge prey-dots resulted from the requirement to cover more “ground” before reaching the target, and thus these targets had a lower encounter rate. This contrasts with work using fish, which indicates a higher encounter rate for group edges (Duffield & Ioannou, 2017). The preferentially targeting of group edges is thought to occur as a consequence of these regions being encountered first by predators seeking groups of prey to attack (Duffield & Ioannou, 2017). However, fish presented with a 2-D prey group (as in Chapters 2 and 3) still present this behaviour (Romey et al., 2007), despite technically not being restricted to encounter edge prey before central prey. This was evident in Chapter 2 but not Chapter 3. It is possible that the targeting of 2-D group edges is due to perception, expectation or a learned strategy. Edges may be approached first as they are perceived from a distance to be the least compact area of a group (Tosh, 2011), or they may be preferentially targeted in response to an association of greater attack success with regions of low local density (Ioannou et al., 2009; Hogan et al., 2017b). The preferential selection of spatially isolated targets is evident in stickleback preying on *Daphnia* (Milinski, 1977), cheetah (*Acinonyx jubatus*) preying on gazelles (*Gazella thomsoni*; Fitzgibbon, 1990) and pupfish (*Cyprinodontidae spp*.) targeting banded killifish (*Fundulus diaphanous;* Morgan and Godin, 1985).

In contrast to Chapter 2, in Chapter 3 the spatial position of prey-dots was unimportant to fish, with only *oddity* influencing target choice. One possible explanation for this is that fish from the two chapters were sourced from different stocks. The stickleback used in Chapter 2 were wild caught, while those in Chapter 3 were obtained from a semi-managed population, housed outdoors but provided additional live and flake food. It is likely that the latter had more prior experience consuming food as it entered the water column, as opposed to approaching live prey that had formed a swarm. When food is added to a tank it typically enters the water column as a high density cluster. Regular feeding in this way may have diminished some of the *confusion effect* associated with density (Milinski, 1979). Whether targeting differences would have persisted past recent experience is not known. However, the Chapter 3 fish would have had regular exposure from early life, when behavioural and sensory phenotypes are highly plastic (Kröger et al., 2003; Knudsen, 2004; Chapman et al., 2010).

6.6 The advantages and disadvantages of choosing conspicuous targets

There is evidence to suggest that the selection of odd prey is beneficial, but how these benefits are conveyed to the predator are uncertain, and were not examined in this thesis. Higher selectivity for odd coloured pigeons in the diet of breeding goshawk pairs was associated with earlier onset of egg laying and better nestling body condition (Rutz, 2012). This finding was interpreted as *oddity* enhancing attack success, however this was based on the assumption that this is how *oddity effect*s function. There was no evidence within the study that targeting odd pigeons resulted in higher attack success. For goshawks, the selection of odd prey increases with age (Rutz et al., 2006; Rutz, 2012) and therefore experience, indicating that there is an advantage to targeting odd prey. Body size was removed from the analyses in Chapters 2 and 3 because it was shown to have no effect on target choice. If size was used as a proxy for age (which may be appropriate, as fish have indeterminate growth; Sebens, 1987), this would suggest that attention capture rather than learned experience contributed to the selection of odd prey in the present study. However there is no way to know what experience of odd prey the fish subjects in this study had prior to testing, and experimental studies rearing fish under different *oddity*-related feeding regimes would be needed to demonstrate the relative contributions of attentional capture and recent and developmental experience.

In Chapter 4, attention capture by *oddity* was a hindrance when the odd item was not the target. For example, the time taken to locate a target was greater when it was further from an odd prey-dot. Stimulus driven attention capture is useful as a means of filtering large amounts of information (Treisman & Gelade, 1980), however occasionally attentional capture by conspicuous prey, or regions of prey groups, can result in suboptimal foraging decisions (Krause and Godin, 1995, Ioannou et al., 2009). The time taken for a predator to approach a prey group (Ioannou et al., 2009), and the preferential targeting of one group over another (Krause and Godin, 1995) have been used to indicate the relative conspicuousness of different groups. Denser group regions are detected faster in pike (Turesson & Bronmark, 2007) and approached faster in stickleback (Milinski, 1977; Ioannou et al., 2009) and humans (Hogan et al., 2017b). In all of these cases, the subsequent attacks launched are less successful than those made towards less dense, but less conspicuous, group regions. It is possible that there is a perceived advantage, which is not realised, of feeding rate being maximised in large, dense groups (Heller & Milinski, 1979). However, it is also possible that the preferential targeting observed in these cases is due to counterproductive attention capture.

Within mixed groups larger *Daphnia* are preferred by stickleback regardless of whether they are odd (Rodgers et al., 2014; Raveh et al., 2019), presumably due to their higher energy content (Nuutinen & Ranta, 1986). Cichlids also show a preference for large over small groups of guppies (Krause & Godin, 1995), and stickleback for large over small *Chironomid* larva (Ibrahim & Huntingford, 1989). In both of the latter cases, this preference is reversed when the smaller of the two prey items become conspicuously more active (Ibrahim & Huntingford, 1989; Krause & Godin, 1995). This evidence is indicative of attention capture playing a counterproductive role in predation. A preference for faster moving prey does not convey any conceivable benefit to a predator, as such prey would be more evasive. However, movement captures attention (Franconeri & Simons, 2003). The likelihood that movement within the field of vision is behaviourally relevant is high (Skarratt et al., 2014). Being evolutionarily wired to attend to conspicuous movement cues is adaptive, however, in cases such as these it unhelpful. The relative benefits of *oddity* in capturing attention and enhancing attack success (Landeau & Terborgh, 1986; Ruxton et al., 2007) may be counteracted to a lesser or greater extent by unhelpful *oddity* cues (Ibrahim & Huntingford, 1989) , but this is yet to be explored fully.

6.7 Further work

Thresholds of *oddity* at both the detection (Chapter 4) and attack (Chapter 2) stage of predation were established in this study, but this generated further research questions. Examining the preferential targeting of odd prey at multiple group sizes would indicate whether *oddity effect*s occur in response to absolute numbers or proportional representation. As is the case with *confusion effect* (Jeschke & Tollrian, 2007), different species may have different thresholds of *oddity*. Exploring and establishing thresholds of *oddity* would pave the way for understanding the selection pressures and cognitive constraints that might lead to these thresholds. If preferential targeting of odd prey results from higher *salience* then *salience* mapping based on photoreception data of different species (Pike, 2018) could predict which prey may be targeted within a group.

The *confusion effect* is attributed to the inability to successfully track and target prey within a group (Ioannou et al., 2008), odd prey are considered to be easier to track and target (Krakauer, 1995; Hogan et al., 2017a). It therefore follows that the ability to track multiple objects should be linked to the limitations imposed by *confusion* and the amelioration of *confusion* through *oddity*. A shared mechanism is proposed for *MOT* and the instant number recognition that occurs for quantities of ≤ 4-5, known as subitising, in humans (Chesney & Haladjian, 2011). While *MOT* has not been demonstrated in non-human species, subitising of moving stimuli has, through the study of non-human numerosity (chimpazees *Pan troglodytes*: Murofushi, 1997; free ranging dogs *Canis lupus familiaris*: Bonanni et al., 2011; guppies: Agrillo et al., 2014). As non-human animals are capable of subitising, an object tracking system should therefore be present through the same visual mechanisms (Chesney & Haladjian, 2011), although this is yet to be explored. A difficulty in enumerating moving over static target objects in the black bear (*Ursus americanus*) was attributed to the lack of complex social structures in this species (Vonk & Beran, 2012). In a non-social species the ability to keep track of group mates would not have been selected for. Through the same logic it could be predicted that that social species would have higher *MOT* capabilities than non-social species.

Throughout this thesis prey were categorised as either being minority (odd) or majority (not-odd). *Oddity* was demonstrated using the luminance contrast of light and dark stimuli. Previous work into the *oddity effect* has also used discrete categories, e.g. large and small (Rodgers et al., 2011; Rodgers et al., 2014), to assign *oddity* status to prey. For colour *oddity*, two distinct phenotypes are used, for example: red and yellow *Daphnia* (Ohguchi, 1978), red and blue *Daphnia* (Rodgers et al., 2013) and silver and blue minnow (Landeau & Terborgh, 1986). Studies into *oddity* and assortative grouping also use two distinct phenotypes, for example black and white mollies (Rodgers et al., 2013) and dark and pale western rainbow fish (Rodgers et al., 2010). However, size and body colouration are not discrete categories, rather they vary on a continuous scale. The wavelengths of the visible spectrum increase from violet to blue to green, and so on (Johnsen, 2012). It is not known at which point along this scale visual differences would become costly as a consequence of the *oddity effect*. Further work could expand on Chapters 2 and 5, where *oddity* was considered as a function of group composition, to look at which point a phenotype becomes different enough to be subject to preferential targeting, for example. The same considerations could be made for the grouping preferences of prey. Work into this area would need to take in to account that perceptual nature of colour, which is subject to change based on factors such as illumination and individual perception (Johnsen, 2012; Brainard & Hurlbert, 2015).

6.8 Conclusion

The importance of *oddity* for overcoming the challenges associated with larger groups was demonstrated at both the detection and attack stage of predation. This is the first study to empirically demonstrate that numerical group size drives the selection of odd prey. This indicates that odd individuals are at an increased risk from preferential targeting by visual predators within larger prey groups.

The identification of low thresholds for *oddity* suggest that an individual that joins a majority unmatched group, raising the representation of a minority phenotype, will benefit minority, and possibly majority, type group members. This indicates that *oddity* *effect*s do not necessarily select for homogenous groups, as *oddity* is only costly when present as a very small minority.

Oddity operates at both the detection and attack stages of the predation cycle. Attentional capture by *oddity* at the detection stage may have consequences for non-odd group members depending on their proximity to odd group-mates. Whether these consequences are positive or negative for majority type group members is dependent on the predator-prey system in question.

6.9 References

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