USING VIRTUAL REALITY TO INVESTIGATE 'PROTEAN' ANTI-PREDATOR BEHAVIOUR

Graham Richardson

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Declaration

I declare that no material contained in this thesis has been used in any other submission for an academic award at this or any other institution. I declare that the thesis is all my own work, except where otherwise stated.

Acknowledgements

Abstract

Prey animals have evolved a wide variety of behaviours to combat the threat of predation, many of which have received considerable empirical and theoretical attention and are generally well understood in terms of their function and mechanistic underpinning. However, one of the most commonly observed and taxonomically widespread antipredator behaviours of all has, remarkably, received almost no experimental investigation: so-called 'protean' behaviour. This is defined as 'behaviour that is sufficiently unpredictable to prevent a predator anticipating in detail the future position or actions of its prey'. In this thesis, I have elucidated the mechanisms that allow protean behaviour to be an effective anti-predatory response. This was explored with two approaches. Firstly, through the novel and extremely timely use of virtual reality to allow human 'predators' to attack and chase virtual prey in three-dimensions from a first-person perspective, thereby bringing the realism that has been missing from previous studies on predator-prey dynamics. Secondly through the three-dimensional tracking of protean behaviour in a highly tractable model species, the painted lady butterfly (*Vanessa cardui*). I explored this phenomenon in multiple contexts. Firstly, I simulated individual protean prey and explored the effects of unpredictability in their movement rules with respect to targeting accuracy of human 'predators' in virtual reality. Next, I examined the concept of 'protean insurance' via digitised movements of the painted lady butterfly, exploring the qualities of this animals' movement paths related to human targeting ability. I then explored how the dynamics of animal groupings affected protean movement. Specifically, I investigated how increasing movement path complexity

interacted with the well-documented 'confusion effect'. I explored this question using both an experimental study and a VR citizen science game disseminated to the general public via the video game digital distribution service 'Steam'. Subsequently, I explored another phenomenon associated with groupings of prey items; the 'oddity effect', which describes the preferential targeting of phenotypically odd individuals by predators. Typically, this phenomenon is associated with oddity of colouration or size. In this case, I investigated whether oddity of protean movement patterns relative to other group members could induce a 'behavioural oddity effect'. Finally, I used a specialised genetic algorithm (GA) that was driven by human performance with respect to targeting prey items. I investigated the emergent protean movement paths that resulted from sustained predation pressure from humans. Specifically, I examined the qualities of the most fit movement paths with respect to control evolutions that were not under the selection pressure of human performance (randomised evolution). In the course of this thesis, I have gained a deeper understanding of a near ubiquitous component of predator prey interactions that has until recently been the subject of little empirical study. These findings provide important insights into the understudied phenomenon of protean movement, which are directly applicable to predator –prey dynamics within a broad range of taxa.

Preface

All authors of the following publications have contributed in various degrees to the research concept, and to the experimental design as well as the final writing of the manuscripts.

Journal publications

Richardson, G., Dickinson, P., Burman, O. H. P., & Pike, T. W. (2018). Unpredictable movement as an anti-predator strategy. Proceedings of the Royal Society B: Biological Sciences, 285(1885), 20181112.

Conference talks

Richardson, G., Dickinson, P., Burman, O. H. P., & Pike, T. W. (2017). 'Investigating Protean Anti-Predator Behaviour Using Virtual Reality', *2017 ASAB Easter Conference*, *University of Liverpool, 5-7 February.*

Richardson, G., Dickinson, P., Burman, O. H. P., & Pike, T. W. (2018). 'Investigating Protean Anti-Predator Behaviour Using Virtual Reality', *2018 European Conference on Behavioural Biology (ECBB), University of Liverpool,* 9-12 *August.*

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1. General Introduction

"Even brute beasts and wandering birds do not fall into the same snares twice."

Jerome – *Letter 54*

1.1 Predator-prey interaction

Predation refers to the act of individuals of one species (predators) locating, capturing, killing, and consuming individuals of another species (prey) for sustenance (Sergio et al., 2014). These interactions between predators and their prey are the prime movers of energy through food chains (Taylor, 1984). They are an important factor in the ecology of populations, determining mortality of prey and birth of new predators. Nearly all animals in nature must avoid predation at some point in their lives, and so predation forms an important evolutionary force (Lima & Dill, 1990). Natural selection favours more effective predators, but it also favours the prey that are best at avoiding predation. This arms race has resulted in the evolution of a vast range of anti-predator adaptations (mechanisms which assist prey organisms by reducing their chances of predation) (Edmunds, 1974). Throughout the animal kingdom, prey organisms have evolved adaptations for every stage of this struggle. Obvious and visible examples of anti-predator defences are physical structures such as shells and spines. Many gastropods and bivalves utilise defensive shells, for example marine snails (*Lirtorina obiusata*) (Lowell, Fletcher, Grahame, & Mill, 1994)

and mussels (*Mytilus edulis*) (Dit Durell & Goss-Custard, 1984) respectively. Examples of spines for defence include the sharp scalpel-like structure on the front of each tail fin in Sohal surgeonfish (*Acanthurus sohal*) (Jawad, 2018) and the spines of porcupines (e.g. Crested porcupine *Hystrix indica*), which are long, stiff, break at the tip, and are barbed to stick into a would-be predator (Vincent & Owers, 1986). Other structures are primarily sexually selected but may also be used as antipredator defences in a secondary role. Examples include the antlers on most male deer species (e.g. red deer [*Cervus elaphus*]) (Clutton-Brock, 1982) and in most cambarid crayfish species, where males have longer and heavier chelae (claws) than females, but are also used in an anti-predator capacity when necessary (e.g. Northern clearwater crayfish [*Orconectes propinquus*] (Stein, 1976). In addition to morphological and physiological anti-predator adaptations, animal behaviour is also subject to the selection pressures induced by predation (Barnard, 1983). As a result, prey organisms have evolved a wide diversity of behavioural mechanisms to combat the threat of predation.

The first line of defence for many prey species is to remain undetected by their predators. There are several means to achieve this. Firstly, many prey organisms are nocturnal, characterized by activity during the night and sleeping during the day. For example, many bat species feed at night to avoid aerial predators active during the day (Duverge, Jones, Rydell, & Ransome, 2000). Prey may also avoid predators by living in burrows, crevices, buildings, tree cavities or other sheltered places, only emerging to feed or perform other vital activities (Barnard, 1983). For example, the naked mole rat (*Heterocephalus glaber*) lives almost exclusively in underground burrows (Kingdon et al., 2013). Little owls (*Athene noctua*) often roost in tree cavities

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which provide protection from predators (Bock et al., 2013). The mutualistic relationship between three unrelated families of sea anemones (*Thalassianthidae, Actinidae, Stichodactilidae*) and clownfishes (belonging to the Pomacentrids family) provide several benefits to one another, including protecting the latter from predators (Roux et al., 2019). If these strategies fail and prey animals are detected, they may respond with further behavioural defences aimed at deterring predators. Alternatively, animals may forgo the anti-predator benefit of avoiding detection by forming groups, which typically increase the chances of detection but provides safety in numbers (Lehtonen & Jaatinen, 2016), allowing group based anti-predator effects, such as 'selfish herding', where individuals under a predatory threat continuously attempt to move toward the centre of the group, where risk of capture is typically lower (Hamilton, 1971).

If a solitary animal is detected, or an individual is singled out or separated from a grouping, many animals are able to make use of patterns of threatening or startling behaviour, to scare off or momentarily distract a predator, thus giving the prey animal an opportunity to escape. This is known as 'deimatic' behaviour, a common example is the peacock butterfly (*Aglais io*) which displays striking, conspicuous patterns on its wings (known as eyespots) when disturbed (Merilaita et al., 2011). Animals may utilise 'pursuit-deterrent' signals in order to convince prey not to pursue them. For example, Columbian black-tailed deer (*Odocoileus hemionus columbianus*) often 'stot' when a predator is particularly threatening. A stot is a type of high jump characterised by stiff legs and an arched back. This is thought to be a signal to predators that the stotting animal would be difficult to catch. As a result, predators may choose to pursue a different prey that is easier to capture (Stankowich

& Coss, 2007). Animals may also create distractions to assist their escape from predators. This strategy is common amongst marine molluscs such as sea hares, cuttlefish, squid and octopuses who can eject a mixture of chemicals, which may mimic food or otherwise confuse predators (Derby, 2007). For example, in response to a predator, the odd bobtail squid, (*Heteroteuthis dispar*) often releases ink, creating a cloud, affecting the predator's feeding senses, causing it to attack the cloud (Dilly & Herring, 2009). Animals may display thanatosis (i.e. 'play dead') as a form of bluff in which an animal feigns death to avoid being attacked by predators seeking live prey, a common example being the North American Opossum (*Didelphis marsupial*) (Francq, 1969). Finally, animals may attempt to flee by any available means, whether by flying, gliding, falling, swimming, running or jumping, according to the animal's capabilities (Edmunds, 1974). Many antipredator behaviours, including those described above have received considerable empirical and theoretical attention and are generally well understood in terms of their function and mechanistic underpinning (Krause & Ruxton, 2002). However, one of the most commonly observed and taxonomically widespread antipredator behaviours of all has, remarkably, received almost no experimental investigation: so-called 'protean' behaviour.

1.2 Protean behaviour

Protean behaviour is broadly defined as behaviour which is "sufficiently unsystematic to prevent a reactor predicting in detail the position or actions of the actor" (Humphries & Driver, 1970). There are a wide variety of forms in which this behaviour can take. For example, distraction displays are common in many bird species (e.g.

Spotted Sandpiper [*Tringa macularia*]) where prey organisms feign injury to draw a predator from a 'prize' (e.g. a clutch of eggs) then escape to their *actual* full ability (which the predator is less likely to be able to predict) at an opportune moment (Armstrong, 1954). Other examples involve morphological features, such as the ability of certain animals to rapidly alter their colouration. When under the threat of predation, the cuttlefish *Sepia officinalis* has been recorded as presenting a morph with conspicuous colour patches (i.e. white body with two black spots), then rapidly darkening its appearance and attempting a rapid escape movement (Holmes, 2010). In this instance, the unpredictability for the predator is derived from the "searching image" of the original colour morph formed during the predators initial contact with the prey (Franck, Impekoven, & Tinbergen, 1967). When this morph has unpredictably changed, the predator is still guided by the now incorrect searching image, confusing its ability to reacquire the prey and potentially losing it. Furthermore, certain prey animals are capable of using vocalisations to introduce unpredictability with respect to their future actions. For example, the dogbane tiger moth (*Cycnia tenera*) can produce ultrasound clicks which can confuse their echolocating predators (e.g. the big brown bat [*Eptesicus fuscus*]). When the bat is about to strike, the clicks induce a sudden and momentary disruption of information processing preventing the bat from predicting the position of the moving moth (Fullard, Simmons, & Saillant, 1994).

Protean behaviours also present in groups of individuals. For example, when flocks of avian prey species 'mob' threatening avian predators (e.g. chaffinch [*Fringilla coelebs*] mobbing raptors such as the tawny owl [*Strix aluco*] [Hinde, 1954]). Each mobbing individual alternates with the others in making brief mock attacks on

the predator whose attention is thus distracted repeatedly so that any counterattack it may attempt is disrupted. The protean element of this behaviour is derived from the difficulty in predicting which individuals will next attempt a mock attack. This can reduce the ability of predators in capturing their prey and can result in predators abandoning the attack completely (Marler, 1958). The effectiveness of the mobbing is further increased by the unpredictable movement patterns of the prey animals within the grouping. Indeed, all of the examples listed above operate in tandem with (or are in advance of) fleeing from a predatory threat, which is the most common response for prey organisms when detecting the immediate threat of a predator (Humphries & Driver, 1970). The most commonly observed protean behaviours are therefore those which involve unpredictable movement patterns of the prey animal. This specific protean behaviour is referred to as protean movement.

1.3 Protean movement

If a prey animal flees from a predator with greater speed than the predator is willing or able to express, it will likely escape. However, in ~90% of predator prey relationships, the predator is the larger of the two (Cohen, Pimm, Yodzis, & Saldana, 1993) and more massive animals tend to be capable of moving at higher speeds than less massive animals (although there is a 'hump' in this relationship with max speed tending to drop for swimming animals > 110 kg, running animals > 100 kg and flying animals > 2 kg [Hirt, Jetz, Rall, & Brose, 2017]). In this common situation where the predator is faster than the prey (and particularly if there is no nearby cover or refuge), the prey must actively respond to the predatory threat and incorporate

unpredictable protean movements into its locomotion and attempt to evade the predator.

Unpredictability can be incorporated into animal movement in a wide variety of ways. Animals may leap (sand hoppers [*Talitrus saltator*] [Humphries & Driver, 1970]), dive (praying mantis [*Parasphendale agrionina*] [Yager, May, & Fenton, 1990]), loop (owlet moths [family *Noctuidae*], geometer Moths [family *Geometridae*] [Roeder, 1962]), zig-zag (dwarf blaasop pufferfish [*Torquigener flavimaculosus*] [Bilecenoğlu, 2005]) or involve darting 'start-stop' movement patterns (Günther's vole [*Microtus socialis*] [Edut & Eilam, 2004]) to attempt to evade predators. Many of these unpredictable elements of movement may be combined to produce a single dynamic protean movement display (e.g. psychodid fly [*Psychoda phalaenoide*] [Humphries & Driver, 1970]) (see Fig.1.1 for visualisations of example protean movement patterns). Protean movements have been reported in a wide range of taxa including reptiles (Eifler & Eifler, 2014), cephalopods (Staudinger, Hanlon, & Juanes, 2011), mammals (Chance & Yaxley, 1950), insects (Hügel & Goerlitz, 2019), malacostracans (Bridger, Bonner, & Briffa, 2015), birds (Major & Dill, 1978) and ray-finned fishes (Reist, 1983). It is important to note that random (and therefore unpredictable) elements are often present in animal movement paths in contexts other than escaping predators (e.g. Lévy flight foraging paths [Benhamou, 2007]). The key distinguishing feature between protean movements and other randomised movement patterns is the primary function of the movement (i.e. anti-predator defence).

While protean movement is frequently observed over a wide taxonomic spread (see Table.1.1), few studies have directly tested the repeated assumption that protean movement can act to decrease predation risk (e.g. Arnott, Neil, & Ansell, 1999; Domenici, Booth, Blagburn, & Bacon, 2008; Edut & Eilam, 2004; Herbert-Read, Ward, Sumpter, & Mann, 2015). Protean movement has also been reported in various social contexts. Most often, protean movement is reported in response to a predatory threat and is defined as 'active' protean movement (Humphries & Driver, 1970). However, protean movements may also be displayed when no predatory threat has been detected. This phenomenon was also defined as 'protean insurance' or 'passive' protean movement by Humphries & Driver (1970). This protean insurance is perhaps most clearly displayed in larger insects such as butterflies, many of which display protean elements in their normal flight and simply exaggerate these elements upon detecting a predatory threat and attempting escape (Humphries & Driver, 1970). However, the qualities of movement that result in effective protean insurance are poorly understood. Additionally, in groups of individuals, the 'confusion effect' (the reduced attack-to-kill ratio experienced by a predator resulting from an inability to single out and attack an individual prey in a group [Krakauer, 1995]) can occur. It has been suggested that protean movement may interact with the confusion effect. To clarify, increasing the unpredictability of turning (i.e. displaying 'more protean' movement) may interact with the confusion effect to result in an additional increase in the overall difficulty of capture. However, the relationship between the confusion effect and protean movement is equivocal, with evidence supporting an interaction between protean movement and the confusion effect resulting in the increasing effectiveness of protean movement

(Scott-Samuel, Holmes, Baddeley, & Cuthill, 2015) and evidence suggesting no relationship between the two (Jones, Jackson, & Ruxton, 2011). Finally, the individuality of movement behaviours can be attenuated in groups, suggesting that conspicuous movements may be preferentially targeted due to the 'oddity effect' (e.g. female mosquitofish [*Gambusia holbrooki*] [Herbert-Read et al., 2013]). This effect is usually associated with oddity in size or colouration of an individual with respect to a grouping resulting in preferential targeting (Blakeslee, McRobert, Brown, & Clotfelter, 2009; Krause & Godin, 2010; McRobert & Bradner, 1998; Wolf, 1985). What is not known is if the same oddity principle applies to conspicuous movement patterns of an individual relative to a grouping. Additionally, almost all direct evidence in support of protean movement uses simulated prey animals. Finally, examinations into how the components of protean movement patterns (i.e. speed, turning angle etc.) contribute to their evasiveness are rarer still.
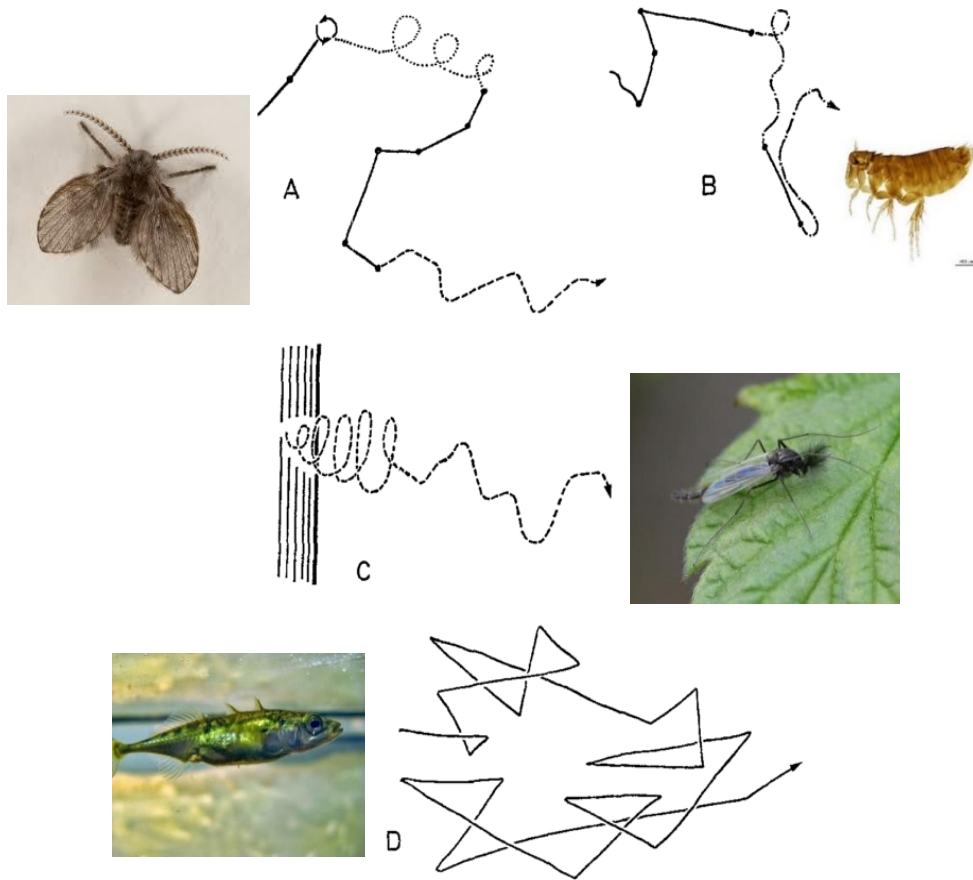
Fig. 1.1 Examples of protean movement of individuals. A) *Psychoda phalaenoides* disturbed by a tactile stimulus. B) Escape reaction of a duck flea, *Ceratophyllus garei*. C) Typical reaction of a chironomid disturbed from its resting place on a tree trunk. D) *Gasterosteus* chased by a merganser duckling. Original image Humphries & Driver, (1970). Animal image credits A-D:
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Table 1.1 Summary of studies that provide support for an antipredator role in protean movement. Table includes the study type (*in virtuo* refers to studies within Virtual Reality [VR]). Also included are the phyla and class of the prey animal in which the protean anti-predator movement was examined or observed. The right column indicates whether the corresponding study quantified whether protean movement resulted in increased effectiveness at evading predators (direct) or observed and reported the behaviour and/ or offered protean movement as an explanation for the unpredictable movement patterns (indirect).

Author(s)	Study Type	Focal animal (species)	Phylum	Class	Support
Berberi, Segre, Altshuler, & Dakin (2020)	*In vivo*	Hummingbirds	Chordata	Aves	Indirect[2]
Bilecenoğlu (2005)	*In situ*	Dwarf blaasop pufferfish (*Torquigener flavimaculosus*)	Chordata	Actinopterygii	Indirect
Bridger, Bonner, & Briffa (2015)	*In vivo*	Hermit crab (*Pagurus bernhardus*)	Crustacea	Malacostraca	Indirect
Chakraborty, Bhunia, & De (2020)	*In silico*	NA	NA	NA	Indirect[3]
Chance & Yaxley (1950)	*In vivo*	Deermice (*Peromyscus* sp.)	Chordata	Mammalia	Indirect
Combes, Rundle, Iwasaki, & Crall (2012)	*In vivo*	Fruit fly (*Drosophila melanogaster*)	Arthropoda	Insecta	Direct
Edut & Eilam (2004)	*In vivo*	Spiny mouse (*Acomys cahirinus*)	Chordata	Mammalia	Indirect
Edut & Eilam (2004)	*In vivo*	Günther's vole (*Microtus socialis*)	Chordata	Mammalia	Indirect
Eifler & Eifler (2014)	*In situ*	Wedge-snouted desert lizard (*Meroles cuneirostris*)	Chordata	Reptilia	Indirect
French (2010)	*In silico*	NA	NA	NA	Direct[3]
Gaddis (1980)	*In situ*	NA	Chordata	Aves	Indirect[2]
Herbert-Read, Ward, Sumpter, & Mann (2015)	*In vivo*	Pacific blue-eye (*Pseudomugil signifer*)	Chordata	Actinopterygii	Indirect
Hügel & Goerlitz (2019)	*In vivo*	Eared moths	Arthropoda	Insecta	Indirect[2]
Humphries & Driver (1970)	*In situ*	NA	NA	NA	Indirect[6]
Jones, Jackson, & Ruxton (2011)	*In silico*	NA	NA	NA	Direct[4]
Kawabata et al. (2020)	*In vivo* / *In silico*	Red seabream (*Pagrus major*)	Chordata	Actinopterygii	Indirect[7]
Major & Dill (1978)	*In situ*	Dunlin (*Calidris alpina*)	Chordata	Aves	Indirect

Major & Dill (1978)	*In situ*	Starling (*Sturnus vulgaris*)	Chordata	Aves	Indirect
Marshall & Orr (1972)	*In situ*	Marine copepod (*Calanus* sp.)	Crustacea	Hexanauplia	Indirect
Miller & Olesen (1979)	*In vivo*	Green lacewing (*Chrysopa carnea*)	Arthropoda	Insecta	Indirect
Reist (1983)	*In vivo*	Brook stickleback (*Culaea inconstans*)	Chordata	Actinopterygii	Indirect
Richardson, Dickinson, Burman, & Pike (2018)	*In virtuo*	NA	NA	NA	Direct[4,5]
Roeder (1962)	*In situ*	Owlet moths [family *Noctuidae*]	Arthropoda	Insecta	Indirect[2]
Roeder (1962)	*In situ*	Geometer Moths [family *Geometridae*]	Arthropoda	Insecta	Indirect[2]
Sandhu, Gulrez, & Mansell (2020)	*In vivo*	Human (*Homo sapiens*)	Chordata	Mammalia	Direct[1]
Santer, Rind, Stafford, & Simmons (2006)	*In vivo*	Migratory locust (*Locusta migratoria*)	Arthropoda	Insecta	Indirect
Staudinger et al. (2013)	*In vivo*	Cuttlefish (*Sepia officianalis*)	Mollusca	Cephalopoda	Indirect
Swingland (1977)	*In situ*	Rook (*Corvus frugilegus*)	Chordata	Aves	Indirect
Tallmark & Evans (1986)	*In vivo*	Brown shrimp (*Crangon crangon*)	Crustacea	Malacostraca	Indirect
Treherne & Foster (1982)	*In situ*	Ocean skater (*Halobates robustus*)	Arthropoda	Insecta	Indirect
Tsutsui, Shinya, & Kudo (2019)	*In vivo*	Human (*Homo sapiens*)	Chordata	Mammalia	Direct[1]
Yager, May, & Fenton (1990)	*In vivo*	Praying mantis (*Parasphendale agrionina*)	Arthropoda	Insecta	Indirect

[1] Simulation with human actors as predators and prey

[2] Multiple species surveyed

[3] Theoretical predator-prey model

[4] Simulation with human predators, digital prey

[5] Subject of chapter 2

[6] Review of protean movement examples in various taxa

[7] Geometric model derived from *in vivo* data

The study by Combes, Rundle, Iwasaki, & Crall (2012) directly supported the notion that protean movement can reduce the chances of predators capturing prey in a real predator-prey system. To my knowledge, this study is unique in that respect, with other studies either providing indirect support, or utilising digital animals (representing either predators, prey, or both). They reported that fruit flies (*Drosophila melanogaster*) attacked on the wing by dragonflies (*Libellula cyanea*) rarely responded with evasive manoeuvres; and were rarely successful when they did. Instead, routine, erratic turns performed by the flies throughout their flight were responsible for the most failed predation attempts (i.e. the fly would turn coincidently when the dragonfly was about to strike, the dragonfly was outmanoeuvred and unable to capture the prey). This study demonstrated that unpredictable protean elements in an animal's movement can reduce the chances of capture by a predator. This study represents a rare instance of direct evidence of protean movement reducing the chances of a prey animal being captured by a predator in a real predator-prey system. Studies in real systems often suggested protean movement as an explanation for observed erratic movement patterns or observed protean movement alongside other protean elements, somewhat confounding the effects of each element on predator evasion (e.g. colour changes or vocalisations in advance of protean movements [e.g. Roeder, 1962; Staudinger et al., 2013]). Although the study by Combes et al. (2012) looked at pursuit and interception, the authors considered these interactions more akin to ambush predation due to the relative speed with which the dragonflies approached their prey. The study is indicative of the effect that a protean turn can have at an opportune time. Less understood are the broader themes regarding the qualities of

protean movement required to be evasive over a larger time frame (i.e. a sustained evasive manoeuvre or pursuit). The current uptick in publications that have directly evidenced the effectiveness of protean movement have primarily used computerised predator-prey systems, which are increasingly popular in the study of predation concepts in behavioural ecology.

1.4   Computerised systems and predation concepts in behavioural ecology

Digital representations of animal movement behaviours have been in use since the late 60's (Rohlf & Davenport, 1969; Watt, 1968) and have been used to study a wide variety of topics in behavioural ecology, including migration (Chang, Miyazawa, & Béguer-Pon, 2016), dispersal (Vuilleumier & Metzger, 2006), foraging (Arora & Singh, 2015; Giuggioli & Bartumeus, 2010; Okuyama, 2020) and swarming behaviours (López-Incera, Ried, Müller, & Briegel, 2020).

Regarding the study of protean movement, French (2010) used a genetic algorithm (GA) to examine the differences in the evolution of effective protean movements (comparable to a terrestrial prey animal escaping a terrestrial predator) at a population level between sexual vs asexual reproduction. A GA is a problem-solving method based loosely on the processes of natural selection. First described by Holland (1975), in recent years the use of GA's in behavioural ecology has grown in popularity (Barta, Flynn, & Giraldeau, 1997; He, Wu, & Saunders, 2006; Huse, Strand, & Giske, 1999; Ruxton & Beauchamp, 2008). French (2010) found that sexual reproduction resulted in a greater variety of protean movement paths (i.e. greater unpredictability of escape paths at a population level). The author then argued that while individuals may show protean variation in their escape paths, population level

variation in protean escape may represent a less evolutionary costly method by which protean variation may emerge. This is supported by some empirical evidence, for example Domenici et al., (2008) who found that when disturbed by a tactile stimulus, cockroaches (*Periplaneta americana*) had a limited number of preferred escape trajectories.

Computerised systems representing animal movements offer many advantages over the use of real animals in the context of studying protean movement. Firstly, prey are artificial, so large sample sizes can be generated while also circumventing any welfare concerns associated with subjecting real animals to predation. Secondly, artificial prey behaviour can easily be manipulated and endowed with whatever behavioural rules that are chosen, something that would be impossible to achieve with live animals. The primary disadvantage of these systems is that observations in real systems must still be utilised to test the real-world validity of any derived data.

1.5 Humans as model predators in ecological studies

The use of surrogate predators has a substantial history in the study of behavioural ecology. For example, in adaptive colouration such as Müllerian mimicry (Beatty, Beirinckx, & Sherratt, 2004), crypsis (Glanville & Allen, 1997) and disruptive camouflage (Stevens et al., 2013). With regards to the study of digital animal movements, human predators have been used to 'hunt' digital prey in studies concerning several associated phenomena including the confusion effect (Tosh, Jackson, & Ruxton, 2006) and motion camouflage (Hall, Cuthill, Baddeley, Shohet, & Scott-Samuel, 2013; Scott-Samuel, Baddeley, Palmer, & Cuthill, 2011). Several

studies have utilised animals to hunt digital prey allowing a finely controlled representation of a real world predator-prey system (e.g. Duffield & Ioannou, 2017; Ioannou, Guttal, & Couzin, 2012; Pike, 2015). However, the use of humans as predators of digital prey (or both predators and prey) offers a more generalist approach but confers several key advantages. Firstly, humans are easily and ethically sampled (Jones et al., 2011). Secondly, humans can receive instructions and manage their behaviour far better than animals (Sandhu et al., 2020). Indeed, protean movement has been studied via the use of human predators in at least three studies (Jones et al., 2011; Sandhu et al., 2020; Tsutsui et al., 2019).

Jones et al. (2011) utilised humans as predators hunting virtual computer-generated prey on a computer screen. Two types of digital prey movements were presented; 'predictable' movements and 'protean' movements. The only difference between protean and predictable prey was in the variance of the turning angle. Protean prey were therefore more likely to turn at a greater angle than predictable prey, making their direction of travel more tortuous. Jones et al. (2011) found that protean prey were harder to catch than those that moved on a smooth trajectory, consistent with an anti-predator benefit for this behaviour.

Tsutsui et al. (2019) conducted one-on-one digital chase-and-escape simulations using humans as predators and prey. The simulations consisted of a predator and a prey object on a computer screen. The prey's objective was to get past a predator to reach safety on the other side of the screen. While most prey animals tend to flee away from predators (Krause & Ruxton, 2002), there are occasions where prey may be forced to move toward and past a predator (e.g. a

wildebeest (*Connochaetes taurinus*) that must pass a Nile crocodile (*Crocodylus niloticus*) in a river crossing [Subalusky, Dutton, Rosi, & Post, 2017]). In their study Tsutsui et al. (2019) found that a consistent protean movement strategy was developed by the human prey that was most often effective. In this strategy, the spatial position at which the prey would change its direction was uniform and therefore unpredictable. The frequency of the turns however was somewhat predictable. The prey would often engage in two direction changes in quick succession to 'wrong-foot' the predator (i.e. a pair of direction changes ~ 200 ms apart, which is below the human visuomotor delay of 200-300 ms [Tsutsui et al., 2019]). The delayed response of the predator could give the prey enough space to reach safety. In this case, the effective protean movement strategy had a predictable element (i.e. the two rapid direction changes) which was mixed with unpredictable elements (i.e. the spatial position of the initial direction change).

Sandhu et al. (2020) conducted a similar study where human participants in the role of both predators and prey were tasked with capturing the prey and escaping the predator, respectively. In three conditions, the prey followed a pattern of movement with varying predictability (predictable, semi-random, and random) and in one condition moved autonomously (user generated). This made four conditions in total. The user-generated condition was found to generate the most effective protean movement patterns (more effective than the randomised condition), thereby indicating that while unpredictability was important in evading predators, the ability of humans to dynamically respond to predator position and maximise perceived distance (which could result in increased predictability) was more important. The results from both Tsutsui et al., (2019) & Sandhu et al. (2020)

indicated that unpredictability alone may not result in effective protean movement, and that a combination of both predictable and unpredictable elements may result in more effective protean movements.

The studies detailed above have contributed greatly to the understanding of the generally understudied phenomenon of protean movement. However, the manner in which stimuli were presented in the three studies detailed above (Jones et al., 2011; Sandhu et al., 2020; Tsutsui et al., 2019) (i.e. moving vertically or horizontally on a flat surface [computer monitor or Perspex board] with limited lateral range), while allowing a high degree of experimental control, lacks realism. To elaborate, the most common behavioural response of prey is to flee *away* from predators (Krause & Ruxton, 2002), which cannot be replicated on a two-dimensional screen (as in Jones et al., 2011). Moreover, the rules given to the virtual prey in Jones et al.'s (2011) study were relatively simple (e.g. 'move randomly within a given angle'). Similarly, in Sandhu et al.'s (2020) study, both predator and prey moved at one unit at a consistent rate (1.17 Hz). Regarding the movement rules, these studies did not explore some of the more intriguing observations that have been made regarding protean anti-predator movement. Specifically, the movement of real animals is dynamic and can show great variation in intra-individual and inter-individual expression (Humphries & Driver, 1970; Shaw, 2020). So how does introducing unpredictability into the rules of digital prey movement (i.e. speed, turn angle, time between turns) change the effectiveness of protean movement with respect to evading predators? Finally, in the case of Tsutsui et al. (2019) and Sandhu et al. (2020) the human controlled predator was in the third-person (i.e. a bird's-eye view) which was a necessity in representing predators and prey in two dimensions

(i.e. on the same plane). However, a three-dimensional simulation of predator-prey interaction would allow for a perspective more representative of a visual predator (i.e. a first-person view). How might the greater realism provided by a three-dimensional perspective to simulations studying animal movement further illuminate the qualities of animal motion that contribute to effective protean movement?

1.6 Virtual reality in research

Virtual reality (VR) refers to immersive simulations that are viewed by a participant (Steuer, 1992). In a VR simulation, an experimenter can maintain full control over the visual and audial stimulus encountered by the participant. Commercially available VR systems may use either VR headsets or multi-projected environments to generate realistic images and/ or sounds that simulate a user's physical presence in a virtual environment. The use of VR in research is a rapidly growing field due to the experimental control over presented stimuli and the commercial availability of the latest generation of VR systems (Cipresso, Giglioli, Raya, & Riva, 2018). Dynamic immersive VR simulations have been used in many disciplines including psychology (O'Hare, Sharp, Dickinson, Richardson, & Shearer, 2018), criminology (van Gelder, Otte, & Luciano, 2014) engineering (Wolfartsberger, 2019), robotics (Williams, Szafir, Chakraborti, & Ben Amor, 2018), healthcare (de Ribaupierre et al., 2014), molecular biology (El Beheiry et al., 2019) and computer science (Dickinson et al., 2019; Hicks et al., 2019). VR has also been utilised in animal behavioural research, which typically use multi-projected environments and operate on restrained animals, providing either visual or tactile feedback (Stowers et al., 2017). Animals tested in VR include zebrafish (*Danio rerio*), mice (*Mus musculus*), and honeybees (*Apis mellifera*), with

biological questions typically regarding visuomotor effects, height aversion, and visual flicker preferences respectively (Schultheiss, Buatois, Avarguès-Weber, & Giurfa, 2017; Stowers et al., 2017; Takalo et al., 2012; G. J. Taylor et al., 2015; Van De Poll, Zajaczkowski, Taylor, Srinivasan, & Van Swinderen, 2015).

Citizen science (CS) is a term that refers to public participation in scientific research. CS has featured in a wide variety of fields including astronomy, oceanography and computer science (Kyba et al., 2013; Lauro et al., 2014; Sullivan et al., 2018). However, the largest impact of CS is in research in biosciences, in particular conservation and ecological research (Kullenberg & Kasperowski, 2016). Notable examples include long-term monitoring of butterfly and bird populations (Bonney et al., 2009; Rüdisser et al., 2017; Wee & Subaraj, 2009). In recent years the internet has been beneficial to published research utilising CS, particularly through gamification (the application of game-design elements and game principles in non-game contexts [Huotari & Hamari, 2012]). Online games have been created to drive research in a number of topics including quantum computing and neuroscience (Ornes, 2018; Tinati, Luczak-Roesch, Simperl, & Hall, 2016). Furthermore, with the increasing availability of affordable VR systems, the commensurate increase in academic studies utilising VR (Pan & Hamilton, 2018; Yung & Khoo-Lattimore, 2019) has begun to include studies involving both VR and CS in scientific research (Striner, 2018; Striner & Preece, 2016). Furthermore, video game digital distribution services such as 'Steam' provide a way to disseminate more complicated games (i.e. those that cannot be played in web browsers) to a wider audience.

1.7 Aims and thesis structure

The overarching hypothesis that this thesis examines is that effective protean movement has a mechanistic underpinning with regards to its effectiveness. This project therefore aims to discern and elucidate said mechanism(s) that allow protean behaviour to be an effective anti-predatory response. This will be explored with two approaches. Firstly, through the novel and extremely timely use of virtual reality to allow human 'predators' to attack and chase virtual prey in three-dimensions from a first-person perspective, thereby bringing the realism that has been missing from previous studies on predator-prey dynamics. Secondly through the three-dimensional tracking of protean behaviour in a highly tractable model species: the painted lady butterfly (*Vanessa cardui*), which is considered to be one of the more conspicuous demonstrators of protean movements (Humphries & Driver, 1970). Furthermore, the inclusion observations from a real system allows the direct comparison to data derived via digital animals. Protean behaviour will be explored in multiple contexts, including individual animals fleeing upon detection of a predatory attack (the most common behavioural response of prey [Krause & Ruxton, 2002]), the passive protean movements that may increase the chances of evading an undetected predatory attack (Humphries & Driver, 1970) and the effect that groupings of individuals have on protean behaviour. Finally, I also conducted an exploratory analysis regarding the optimisation of protean movements under sustained predation pressure representing the processes with which effective protean movement strategies may emerge in animal systems.

This project has built on a technique that has been used widely and successfully to study adaptive prey behaviour: the use of humans 'predating' artificial computer-controlled prey (Jones et al., 2011; Tosh et al., 2006). However, I have overcome the limitations imposed by traditional two-dimensional displays by utilising the recent development of commercially available VR systems, which can be used to present stimuli that appear to move in three-dimensional space. The simulations developed will be directly analogous to, and based upon, those routinely used to study predator-prey behaviour (e.g. Jones et al., 2011; Pike, 2015), but will allow the incorporation of movement in three dimensions, thereby adding realism by both having digital prey items move away from the predator and representing the predators perspective as closer to that of a visual hunter (i.e. from the first person). Furthermore, three dimensional movement allows the representation of movement paths analogous to swimming or flying animals, which constitute a large body of indirect reports on protean movement (Acharya & Fenton, 1992; Bilecenoğlu, 2005; Corcoran & Conner, 2016; Dawson, Kutsch, & Robertson, 2004; Fullard et al., 1994; Hügel & Goerlitz, 2019; Kawabata et al., 2020; Reist, 1983).

This thesis consists of five data chapters that explore the mechanisms that allow protean behaviour to be an effective anti-predatory response. In <u>chapter two</u>, I utilised human participants 'preying upon' digital prey in VR. I characterised how introducing unpredictability into the movement parameters of simulated prey affected the efficacy of protean movement with respect to the targeting ability of human predators. This chapter also functioned as a proof of concept regarding the use of VR in the study of adaptive behaviour. I hypothesised that increased protean variation in the movement characteristics would increase the targeting difficulty for

human participants acting as predators. In <u>chapter three</u> I examined 'protean insurance' movement (*sensu* Humphries & Driver, 1970). This behaviour is frequently reported but there is little direct evidence that these movements reduce the ability of predators to target and capture prey. This chapter therefore aims to address that gap in the literature. I quantified the effectiveness of protean insurance in a real animal by examining the qualities of digitised movement paths of painted lady butterflies (*Vanessa cardui*) with respect to how human participants were able to target them in VR. I hypothesised that the characteristics of butterfly flight paths would predict the overall effectiveness of the butterfly in terms of avoiding targeting by human participants. Chapters four and five examined interactions between group associated effects and protean movement. In <u>chapter four</u>, I investigated the interaction between the group size dependent confusion effect and protean movement with respect to human participants' ability to target or capture simulated prey items. I hypothesised that there would be a significant interaction between the size of a group of protean prey items and their movement path complexity that would affect the ability of human predators to target or capture prey items. In <u>chapter five</u>, I investigated the oddity effect in relation to protean movement. Specifically, I hypothesised that differences in protean movement expression of one individual relative to several other individuals presented simultaneously would induce a behavioural oddity effect resulting in preferential and more accurate targeting by human predators of the behaviourally odd individual. Finally, <u>chapter six</u> was an exploratory analysis into the optimisation of protean behaviour in a simulated animal system. I developed a human performance based genetic algorithm (HPBGA) using the same principles as standard GA (Mitchell, 1999), but with the fitness of a protean

movement path evaluated via the ability of a human participant to target the moving digital prey item. This will cause the protean movement paths to be optimised relative to the behaviour's ability to evade human participants acting as 'predators'. The qualities and variation within the resultant optimised paths were analysed and compared to control evolutions not dictated by human performance. I hypothesised that the protean movements that emerged from the HPBGA would be significantly more effective than those in the control groups.

In summary, this thesis has examined and evaluated the near ubiquitous, but understudied phenomenon of protean movement in animal systems. I have explored the subject in several relevant biological contexts including both active and passive behavioural responses, and the effect of groupings and individuals. I have employed several novel approaches including the use of digital prey in VR and a human performance-based evolutionary algorithm and have demonstrated their use as tools in the study of adaptive behaviour.

2. The efficacy of 'protean' anti-predator behaviour

Parts of this chapter have been published:

Richardson, G., Dickinson, P., Burman, O. H. P., & Pike, T. W. (2018). Unpredictable movement as an anti-predator strategy. Proceedings of the Royal Society B: Biological Sciences, 285(1885), 20181112.

In this chapter, all experimental work and data analysis was carried out by myself. Certain passages of the introduction and discussion were co-written with the authors listed on the publication. This chapter differs from the journal article in that I have updated the introduction and discussion to include recently published relevant literature.

2.1   Chapter Abstract

Prey animals have evolved a wide variety of behaviours to combat the threat of predation, and these have been generally well studied. However, one of the most common and taxonomically widespread antipredator behaviours of all has, remarkably, received almost no experimental attention: so-called 'protean' behaviour. This is behaviour that is sufficiently unpredictable to prevent a predator anticipating in detail the future position or actions of its prey. In this data chapter, we used human 'predators' participating in 3D virtual reality simulations to test how protean (i.e. unpredictable) variation in prey movement affects participants' ability to visually target them as they move (a key determinant of successful predation). We found that targeting accuracy was significantly predicted by prey movement path

complexity, although, surprisingly, there was little evidence that high levels of unpredictability in the underlying movement rules equated directly to decreased predator performance. Instead, the specific movement rules differed in how they impacted on targeting accuracy, with the efficacy of protean variation in one element depending on the values of the remaining elements. These findings provide important insights into the understudied phenomenon of protean antipredator behaviour, which are directly applicable to predator - prey dynamics within a broad range of taxa.

2.2   Introduction

As detailed in the general introduction, there are a wide variety of anti-predator behaviours that have received considerable empirical and theoretical attention and are generally well understood in terms of their function and mechanistic underpinning (Krause & Ruxton, 2002). However, the frequently observed and taxonomically widespread antipredator behaviour known as 'protean' movement (movement that is sufficiently unpredictable to prevent a predator from anticipating the future position of its prey [Humphries & Driver, 1970]), has until recently, received comparatively little attention (Jones et al., 2011; Sandhu et al., 2020; Tsutsui et al., 2019).

In their study, Jones et al. (2011) found, using human subjects 'preying upon' computer-generated moving prey, that individual prey items were harder to catch when their turning angles were drawn randomly from a relatively wide angular range (which they classed as 'protean') than when their turn angles were selected (also randomly) from a relatively narrow angular range (which they classed as

'predictable'). This elegant study therefore provided clear evidence that incorporating protean elements into an animal's movement can have positive anti-predator benefits, although by focussing solely on turning angle it fails to take into account that an animal's movement could be considered protean in various different ways. For example, animals may show unpredictable changes in speed or the distance travelled before turning, alongside (or even instead of) unpredictable turning angles; both of which would be predicted to make an animal's future position harder to predict. Furthermore, because in Jones et al's (2011) study all prey items incorporated some element of unpredictability into their turns, it is unclear what would happen if prey moved in predictable, but non-trivial, ways. This could occur, for instance, if movement parameters such as turning angle were fixed, rather than protean, and has been highlighted as a putatively protean escape behaviour in the spiralling take-off flight of Chironomid midges (Humphries & Driver, 1970).

This notion is supported to some extent by Sandhu et al. (2020) who studied human-controlled predators attempting to capture human-controlled prey on a two-dimensional surface. They found that the paths generated by humans (acting as prey) were less predictable than random computer-generated paths, but were more successful at evading predators. In a similar study utilising human as both predators and prey, Tsutsui et al. (2019) found that the most effective protean movement patterns that human 'prey' engaged in displayed a predictable element (i.e. two rapid direction changes in quick succession) which was most effective at evading human 'predators'. In both studies, a mixture of predictable and unpredictable elements of movement by human controlled prey resulted in the most effective protean movement with respect to evading human controlled predators. However, none of

27

the studies detailed above investigated the specifics of how unpredictability in individual characteristics of movement affected how difficult the protean prey was to capture. Pulling apart the effects of these different movement elements is crucial to furthering our understanding of how a broad range of species respond to potential, and real, threats of predation.

Additionally, the manner in which stimuli were presented in the aforementioned studies (i.e. moving vertically or horizontally on a computer monitor [Jones et al., 2011; Tsutsui et al., 2019] or Perspex board [Sandhu et al., 2020] with limited lateral range), while allowing a high degree of experimental control, lacked realism. In particular, the most common behavioural response of prey is to flee *away* from predators (Krause & Ruxton, 2002), which cannot be rendered from the perspective of a predator in two dimensions. Virtual Reality (VR) has been used as a research tool in several fields including computer science and psychology for over 20 years (Dickinson et al., 2019; Hicks et al., 2019; Hoffman, 1998; O'Hare et al., 2018; Slater et al., 2006)**.** Furthermore, with recent releases of several commercially available VR devices, they are increasingly accessible to researchers, facilitating an uptick in publications utilising these systems (Cipresso et al., 2018). VR simulations of animal movement allows virtual items to move in three dimensions relative to an observer, thereby bringing the realism that has been missing from previous studies on predator-prey dynamics, in addition to allowing the representation of flying and swimming protean prey (both of which are frequently observed as engaging in protean movement (e.g. Bilecenoğlu, 2005; Hügel & Goerlitz, 2019).

In this study, I used human 'predators' playing a 3D VR simulation to test how protean variation in one or more movement elements (speed, the distance travelled between turns, and turn angle) influenced a predator's ability to track the prey item as it moved (a key determinant of successful predation; [Olberg, Worthington, & Venator, 2000]), relative to prey that exhibited movement elements with fixed (and hence potentially predictable) values. I predicted that, as the number of movement elements that exhibited protean variation increased, this would result in increasingly unpredictable prey movement paths which would be more difficult to target.

2.3   Methods

2.3.1   Simulations

All simulations were created in the Unity3D game engine running on a Microsoft Windows PC, and built to run on a Samsung Galaxy S7 smartphone using the Samsung Gear VR system. Unlike simulations on a standard computer screen, where movement is confined to a restricted 2D space, within VR the participant can observe a full 360° 3D environment. This allows both a greater range of motion (e.g. objects can potentially move behind as well as in front of the participant) and, crucially, the third dimension (allowing objects to be perceived as moving away from the participant). Simulations consisted of a black sphere (the 'prey') moving in a 3D virtual space centred on the participant. The prey had a radius of 0.1 m and was presented against a homogenous white background to maximise contrast. Prey movement consisted of a series of steps during each of which it travelled in a straight line in 3D space before turning and moving off on a different trajectory. This pattern of movement is commonly used in animal movement models and is characteristic of

the movement patterns of a wide variety of species (Bovet & Benhamou, 1988; Couzin, Krause, James, Ruxton, & Franks, 2002; Kareiva & Shigesada, 1983). Movement of prey in the simulation was therefore determined by three parameters: the distance travelled in a straight line between turns (hereafter termed 'distance'), the time taken to travel over this distance ('speed') and the angle turned within a cone centred on the prey's direction of travel ('angle'). I considered that each of these parameters could be either 'fixed' (that is, the value assigned to a given prey item was randomly chosen but remained constant throughout a trial; see below) or 'protean' (the parameter value was randomly chosen each time the prey performed a particular behaviour, e.g. each time it turned). As this initial study represented a proof of concept regarding the use of VR in the study of adaptive behaviour, as well as aiming to provide direct evidence in support of the effectiveness of protean movement, the values used for the movement parameters were decided through pilot experiments. Later studies utilised values that were derived from real animal data. The specific values used were based on those obtained from pilot experiments, and were as follows: distance could take fixed values of either 1 m or 5 m (termed 'short' and 'long', respectively) or a protean value drawn from a uniform distribution on [1 m, 5 m]; speed could take fixed values of either 1 ms^{-1} or 3 ms^{-1} (termed 'slow' and 'fast', respectively) or a protean value drawn from a uniform distribution on [1 ms^{-1}, 3 ms^{-1}]; and angle could take fixed values of either 0.1π radians or 0.5π radians (termed 'narrow' and 'wide', respectively) or a protean value drawn from a uniform distribution on [0.1π radians, 0.5π radians]. In total, this resulted in 27 possible combinations of fixed/protean movement elements (e.g. short distance, fast speed and protean angle, and so on).

Within the simulation, participants were free to look around the virtual environment and were able to interact with objects within it in real time. A small, red circle (the reticle) was superimposed onto the centre of the participants' field of view. This reticle provided a point of reference for the participant to facilitate object tracking and allowed interaction between the participant and objects within the simulation.

2.3.2 Experimental protocol

A total of n = 40 participants took part in this study (20 females and 20 males, with a mean age of 20.7 [range, 18 to 28]), all of whom were students of the University of Lincoln. Before providing consent to take part in the study, participants were given written information on the general aims of the study (although not the specific hypotheses being tested), what they would be asked to do, and the approximate time required to complete the study. Their age and gender were reported (but not linked to their experimental data). This project was approved by the College of Science ethics committee at the University of Lincoln (reference CoSREC265).

When participants put on the headset to begin the simulation, they were presented with a series of simple text instructions to familiarise them with the VR environment and demonstrate how to interact with objects within it. Participants were also allowed to take part in as many 'acclimation trials' as they wanted which were present in order to control for any learning effect. These trials consisted of a prey item moving in a simple fixed path and allowed participants to familiarise themselves with the act of tracking an object whilst wearing the headset. Participants typically took part in fewer than three acclimation trials, regardless of their level of

prior experience with VR. Each experimental trial presented the participant with one prey item to track. At the start of each trial, the prey was coloured red and appeared at a fixed default position (5 m directly in front of the participant) and trajectory (facing directly away from the participant). To start each trial, the participant used their head movements to position the reticle over the prey for 3 s. The prey item then turned from red to black to indicate that the trial had started, and began to move based on the combination of fixed/protean movement rules it had been allocated for that particular trial. Participants were instructed that their task was to constantly track the prey item, by maintaining the reticle as close to its centre as possible, as it moved around the virtual environment. As the prey item was being represented in three-dimensions, the objects apparent size would increase, or decrease based on the distance from the observer. Each trial lasted 10 s and there were 27 trials in total per participant (one for each possible combination of fixed/protean parameter values). The order of these trials was randomised for each participant.

2.3.3 Data collection

Data on prey location (its Cartesian coordinates in 3D space) and the participant's head orientation (a 3D vector passing through a point between the participant's eyes and towards the reticle) were collected every 0.02 s throughout each trial, and stored in anonymised text files. At each time step, I subsequently calculated the minimum distance between a 3D point representing the centre of the prey and a 3D vector (ray) indicating the participant's head orientation. This point would always be a point orthogonal to the prey centre along the ray. If the reticle was directly over the centre of the prey this distance would be zero, and would increase with as the reticle moved

further away from the prey's centre. This distribution of distance values was used to calculate the mean distance from the centre of the prey over the 10 s of each trial, as a measure of overall tracking accuracy (where a lower mean distance indicates better overall accuracy) and therefore the overall effectiveness of prey 'behaviour' in terms of avoiding predation.

I also used the data on prey location to compute a measure of prey movement path complexity in each trial, using the information-theoretic approach described by Herbert-Read et al. (2015). This method assigns a numeric value to each path, such that more complex paths receive higher values, and so provides an objective measure of how 'protean' each movement path was. In brief, I constructed an embedding matrix $\mathbf{M}$ containing the 3D positions of the prey over the time window $t, t + 1, \ldots, t + n$ (where here n was simply the total number of positions recorded during each 10 s trial). The x component of the embedding matrix $\mathbf{M}_x$ was derived from the x coordinates of the positions, such that

$$\mathbf{M}_x = \begin{bmatrix} x_t & x_{t+1} & \cdots & x_{t+n/2} \\ \vdots & \vdots & \ddots & \vdots \\ x_{t+n/2} & x_{t+n/2+1} & \cdots & x_{t+n} \end{bmatrix}, \tag{2.1}$$

with $\mathbf{M}_y$ and $\mathbf{M}_z$ derived similarly from the y and z coordinates, respectively. The full embedding matrix is then simply given by $\mathbf{M} = \begin{bmatrix} \mathbf{M}_x \mathbf{M}_y \mathbf{M}_z \end{bmatrix}$. I next subtracted the mean from each column of $\mathbf{M}$, before extracting the vector of singular values s from its singular value decomposition. Each singular value was normalised by dividing it by the sum of all singular values, to give $\hat{s}$, and the complexity of the movement path, H, taken as the entropy of the distribution of the singular values

$$H = -\sum_{i=1}^{n} \widehat{s_i} \log_2 \widehat{s_i}.$$

(2.2)

Representative movement paths, of varying complexity, are given in Fig.2.1.
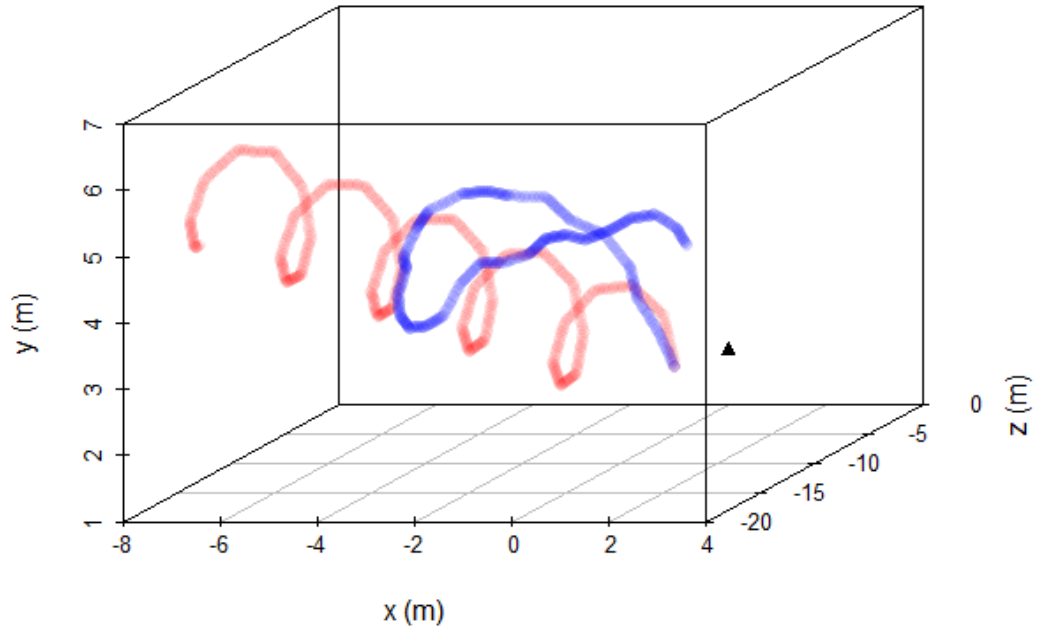
Fig. 2.1 Representative movement paths from a prey with all fixed movement parameters (red; which has a path complexity of 1.53) and a prey with all protean movement parameters (blue; which has a path complexity of 2.29). The black triangle denotes the location of the participant's head in each case, and all prey start from the same position.

2.3.4 Statistical analysis

All analyses were conducted using general linear mixed-effects models (glmm) in R version 3.3.2, using the lmer function in the lme4 package (Bates, Mächler, Bolker, & Walker, 2015). I first tested whether path complexity predicted tracking accuracy, regardless of the specific movement rules underpinning each path. Log_{10}-transformed tracking accuracy was included as the dependent variable, with path complexity as a continuous predictor and trial order as a covariate to control for

possible learning or fatigue effects over consecutive trials. Each participant's anonymous identifier was included as a random effect to control for repeated data from the same individual. Significance was determined by comparing the full model to a reduced model lacking the term of interest using a likelihood ratio test (Crawley, 2005). The validity of the model assumptions was confirmed by visually assessing the normality of the model residuals.

I next considered how the number of protean elements making up the movement rules for each path (which could range from 0, when all three movement parameters had fixed values, to 3, when all three parameters were protean) affected both path complexity and participant performance. Either $\log_{10}$-transformed tracking accuracy or $\log_{10}$-transformed path complexity was included as the dependent variable, with the number of protean movement elements as a fixed factor. As above, I also included trial order as a covariate and each participant's anonymous identifier as a random effect. As I would predict systematic trends in the dependent variable as the number of protean movement elements increased, I additionally fitted polynomial (linear, quadratic and cubic) contrasts over successive levels of the fixed factor. For the analysis involving tracking accuracy, I tested whether the mean tracking distance was significantly different from 0.1 (the radius of the prey's body) by including an offset of 0.1 in the model and testing the significance of the intercept.

Finally, I considered whether the values assigned to the movement parameters predicted participant performance. Each model included $\log_{10}$-transformed tracking accuracy as the dependent variable, and the three movement parameters (distance, speed and angle, each with three levels [high, low and

protean]), along with their three-and two-way interactions, as fixed factors. As above, I included trial order as a covariate and each participant's anonymous identifier as a random effect. In each case, a global model was initially fitted containing all explanatory variables and their interactions. A final model was then determined by stepwise exclusion of the least significant terms, starting with the non-significant highest order interactions and then non-significant main effects. The resulting minimum adequate model is presented. For significant factors I also tested for differences between factor levels using planned treatment contrasts, in which protean movement (the reference group) was compared to each of the other two levels. This allowed us to specifically test the relative efficacy of protean movement, compared to fixed movement strategies. Full model outputs for all analyses are included in Appendix A.

2.4   Results

2.4.1   Path complexity

The complexity of prey movement paths significantly predicted participant performance, with participants exhibiting poorer accuracy (i.e. having a greater mean distance from the prey's centre) as path complexity increased (glmm: $\chi^2(1) = 88.01$, $p < 0.001$; Fig.2.2a). Moreover, path complexity itself was significantly predicted by the number of protean elements in the movement rules underpinning it ($\chi^2(3) = 956.01$, $p < 0.001$), with an increasing number of protean elements resulting in increased path complexity (cubic contrasts: $p < 0.001$; Fig.2.2a,b). This in turn had a significant (although modest) effect on participants' ability to accurately track prey ($\chi^2(3) = 24.07$, $p < 0.001$; Fig.2.2a,c), with the mean distance from the prey's centre

increasing linearly (and tracking accuracy thereby reducing linearly) as the number of protean movement elements rose (linear contrasts: p = 0.002; Fig.2.2c). There was, however, considerable variation within these categories. In particular, even though prey with 0, 1 or 2 protean movement elements contained exemplars that were comparatively easy to track (i.e. on average participants were able to maintain the tracking reticle within the prey's 'body'; Fig.2.2c), tracking accuracy was comparatively poor for the majority of prey items across all categories (including the category with 0 protean movement elements). As such, the mean tracking distance was considerably outside the prey's body in each category, on average (all p < 0.001; Fig.2.2c). This suggests that rather than tracking accuracy being simply a function of movement path complexity, the specific movement rules underpinning them may be important.
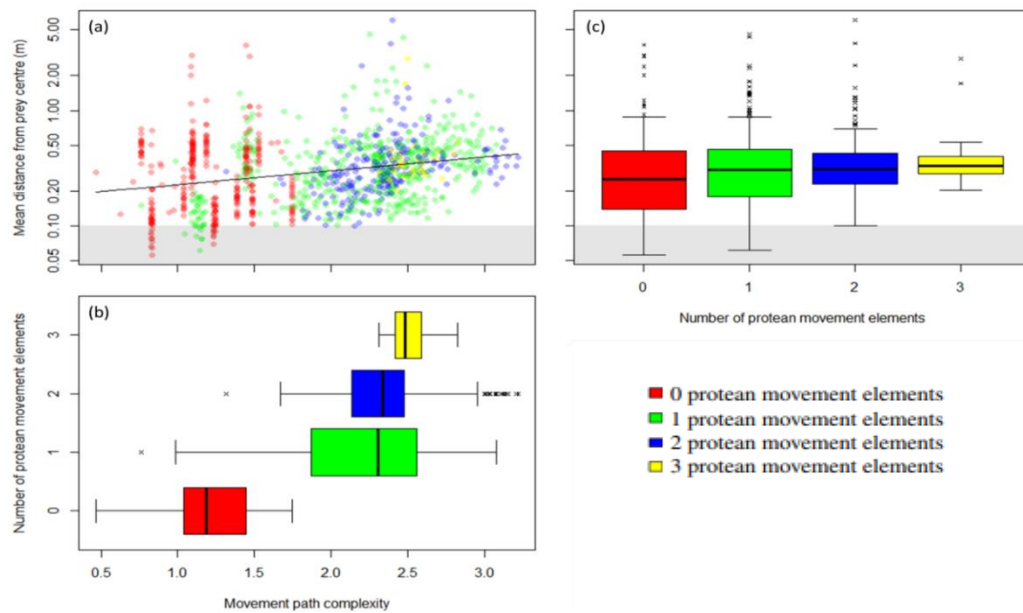
Fig. 2.4 (a) Targeting accuracy (measured as the mean distance from the centre of the prey item over the course of a trial) as a function of movement path complexity. Higher values along the x-axis denote more complex movement paths, while higher values along the y-axis denote poorer targeting accuracy. Note the log scale on the y-axis. Each data point represents a single simulated prey item, and is coloured according to how many protean movement elements it had (0, red; 1, green; 2, blue, and 3, yellow). The solid line denotes the glmm model fit, and the grey shaded area indicates distances within the 'body' of the prey item. For any data point within this shaded area, participants therefore managed to maintain the tracking reticle over the prey's body throughout the entire trial, on average. (b) Movement path complexity as a function of the number of protean movement elements, and (c) tracking accuracy as a function of the number of protean movement elements. Thick lines denote the median, boxes the interquartile range, lines the range of the data, and crosses denote potential outliers (points 1.5 times the interquartile range above the upper quartile and bellow the lower quartile). Box colours correspond to the point colours in (a).

2.4.2   Movement rules

When considering the specific movement rules underpinning prey movement, and hence contributing to the observed variation in path complexity, tracking accuracy was significantly predicted by a single interaction between the speed at which the prey moved and the angle at which it turned ($\chi^2(4) = 22.06$, $p < 0.001$). Specifically,

regardless of whether turning angle was narrow, protean or wide, accuracy was always significantly poorer for prey moving at high speeds than those exhibiting protean variation in speed (treatment contrasts: all p < 0.001) and significantly poorer for protean speeds compared to low speeds (all p < 0.001) (Fig.2.3). However, the relationship between tracking accuracy and turning angle differed depending on the speed of movement: at low speeds, accuracy was significantly poorer when prey turned at protean compared to narrow angles (p < 0.001); at protean speeds, there was no difference in accuracy between turn angles; while at high speeds accuracy was significantly poorer when prey turned at protean angles compared to both narrow (p < 0.001) and wide angles (p = 0.024) (Fig.2.3).
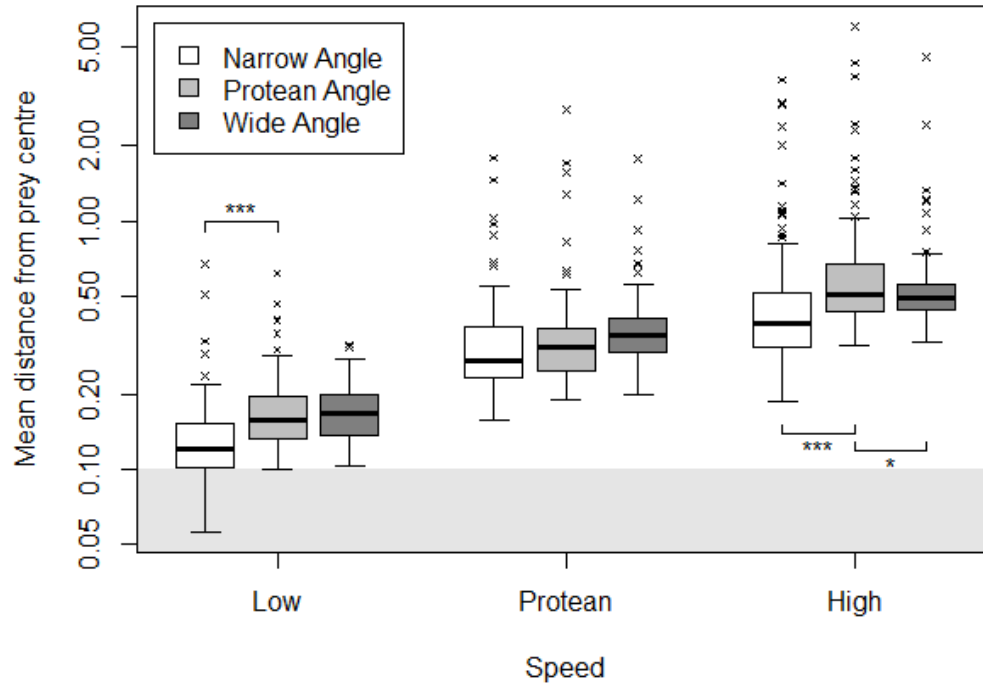
Fig. 2.7 Targeting accuracy (measured as the mean distance from the centre of the prey item over the course of a trial) as a function of Speed (which was categorised as Low, Protean or High) and Angle (which could be either Narrow, Protean or Wide); please see text for full details. Higher values along the y-axis denote poorer targeting accuracy (note the log scale). Thick lines denote the median, boxes the interquartile range, lines the range of the data, and crosses denote potential outliers. The grey shaded area indicates distances within the 'body' of the prey item. Asterisks (*) denote significant differences between levels of Angle at each given level of Speed: * $p < 0.05$; *** $p < 0.001$.

2.5 Discussion

Previous studies have found that prey exhibit increased movement path complexity following a simulated threat (e.g. Herbert-read et al., 2015; Schaerf, Dillingham, & Ward, 2017) with the (untested) assumption being that this increased complexity makes tracking the prey harder, resulting in a reduced chance of predation. Here, I tested this assumption directly by quantifying the ability of human predators to track

virtual prey which differed in the unpredictability of their underlying movement rules, and hence exhibited variation in their resultant movement path complexity. Our results provide direct empirical support for the overall prediction that increased path complexity results in a reduced ability to accurately track prey, although, surprisingly, there was little evidence that high levels of unpredictability in the underlying movement rules equated directly to decreased predator performance. Indeed, prey items that displayed no protean variation in their movement elements at all (and which typically travelled along a putatively 'predictable' spiralling path; e.g. see Fig.2.1) were found to be as difficult to track as prey exhibiting protean variation in all three movement elements (which moved along far more tortuous paths). This is consistent with the findings of Sandhu et al. (2020) who demonstrated that the most effective protean movements taken by humans acting as prey tended to be more predictable, yet more effective than randomised paths. This may also go some way to explain the evolution of spiralling take-off behaviours observed in some insect species (Humphries & Driver, 1970), which may be as effective as the more classically 'protean' erratic zig-zag-type behaviours in evading predators. It also suggests that the mathematical predictability of movement (as encompassed here by our measure of movement path complexity), while a good general predictor of predator performance, ignores the importance of specific movement parameters. Interestingly, here I found that the interaction between movement speed and turn angle was the best predictor of predator performance, while the distance between turns was of limited importance (and not included in the minimum adequate model). More specifically, the relative efficacy of turning behaviour (i.e. whether turns were narrow, protean or wide) differed as a function of speed, with the most effective

protean behaviour involving a mix of protean and fixed elements (in this case high speeds and protean turn angles, regardless of distance travelled). This demonstrates that in terms of efficacy, the 'most protean' behaviour may not always be as effective as combinations of protean and fixed elements.

Our understanding of prey escape decisions has been advanced greatly by considering the fitness costs and benefits of escape, and economic models of escape behaviour have been used to provide qualitative predictions about aspects of escape behaviour (Cooper & Blumstein, 2015). In these models, the costs of escaping typically refer to the lost opportunities of engaging in other behaviours (such as feeding and engaging in social activities including courtship, mating and territorial defence), and the costs of escape are often considered relatively insignificant (Cooper & Frederick, 2007). However, the energetic and/or cognitive costs of maintaining behaviours at the extremes of an animal's abilities, such as travelling at high speeds or turning at wide angles (Cooper & Frederick, 2007; French, 2010; Taylor, Schmidt-Nielsen, & Raab, 1970; Wilson et al., 2013), or, in the case of protean behaviour, behaving unpredictably (Paolo Domenici et al., 2008; Jones et al., 2011) could be considerable. Animals may therefore be expected to optimise the trade-off between the increased chances of avoiding predation and the costs of engaging in protean behaviour. Our results suggest that engaging in escape behaviour that is potentially less cognitively or energetically challenging, but equally efficacious in terms of predator avoidance (such as spiralling), may offer animals a solution to this trade-off. However, the specific ecological conditions that allow the evolution of these different types of behaviour are still to be established.

Literature examples of real-world predator-prey pursuits show a great variation in strategies that vary based on several factors (e.g. the type of predator [solitary or pack hunters] or the difference in size between predator and prey). For example, prey pursued by a single predator tend to use sharp turns (Cooke, 2008) while prey fleeing from multiple predators will often make few or no turns and try to outrun them (Handcock et al., 2009; Saunders, Kay, & Nicol, 1993). However, active evasion of predators may not be the only successful strategy: for example, Combes, Rundle, Iwasaki, & Crall (2012) reported that fruit flies (*Drosophila melanogaster*) attacked on the wing by dragonflies (*Libellula cyanea*) rarely responded with evasive manoeuvres; instead, the flies performed sharp turns that were unpredictable in the timing of their occurrence during flight (i.e. 'passive' protean movement [*sensu* Humphries & Driver, 1970]) which were responsible for more failed predation attempts than active evasive manoeuvres (i.e. movements in direct response to the detection of a predatory threat). I note, though, that whether prey adopt an active or passive anti-predator strategy may depend strongly on the prevailing environmental conditions: the former is likely to be better when predation pressure is constant, or at least predictable; the latter when predation is variable or difficult to predict. The fact that the results from our virtual study into protean behaviour are in agreement with those from a real-life system highlights the benefits of a virtual approach in the study of adaptive prey behaviour.

For example, the use of easily manipulable artificial prey circumvents animal welfare concerns and allows the rapid generation of large sample sizes. Furthermore, our novel approach to this study through the use of VR allowed targeting within a three-dimensional space, allowing prey to flee *away* from a predator (the most

common behavioural response of a fleeing animal (Krause & Ruxton, 2002) and put the perspective of the predator into the first-person, thereby conferring a greater degree of realism over methodologies representing animal movement on two-dimensional computer screens (e.g. Jones et al., 2011), at least for simulated animals that 'fly' or 'swim' within a 3D environment. Quantifying the material impact of the use of VR in this study into adaptive behaviour (as opposed to a two-dimensional approach) is difficult. The primary aim of simulations are to imitate a situation or process as accurately as possible while retaining full experimental control over the conditions of the simulation. VR facilitates increased realism, thereby increasing the accuracy of simulations of protean movement efficacy in three dimensions.

In summary, I can draw several general conclusions about protean behaviour from this study. Firstly, incorporating protean variation into a prey's movement can improve the chances of escaping predators; however, more important with respect to avoiding predation were the interactions between these different movement rules. Interestingly, here I found that the 'most protean' behaviour was not the most effective at avoiding predation. In fact, the most effective behavioural strategy incorporated a combination of protean and fixed elements. Since the publication of the study featured in this chapter (Richardson et al., 2018), this finding has been supported in two other instances (Sandhu et al., 2020; Tsutsui et al., 2019), but the influences of unpredictability in individual movement characteristics on the ability of predators to capture protean prey did not feature in these studies. To put the results of this study into a broader context, here I have provided strong experimental support for the widely-held assumption that protean strategies can reduce chances of predation, and have determined how the individual behavioural rules that make

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up prey movement can interact to affect the overall efficacy of protean behaviour. Our virtual methodology into the study of adaptive behaviour, combined with the parallels between our results and those from real-world systems demonstrates the utility of this approach. In this chapter, using simulated animal movements, I have demonstrated evidence to support the widely held assumption that protean movement makes animals more difficult to target. Chapter two expands on this finding by testing a similar assumption by examining the movements of real animals.

3.   Protean Insurance in Butterfly Movements

3.1   Chapter Abstract

The ability to detect a predatory threat and respond with evasive manoeuvres is a widely reported phenomena. However, prey items are not always able to detect looming predators that pose a threat. One possible adaptive behaviour in response to this predator-prey context is what is known as 'protean insurance', where the default movements of a prey animal are erratic, which may result in the fortuitous evasion of an undetected predator via a change in flight trajectory. However, the phenomenon of protean insurance is little studied with regards to its existence and efficacy (i.e. how flight characteristics contribute to effective evasion). This chapter utilised digitised movements of painted lady butterflies (*Vanessa cardui*), which human participants targeted in virtual reality as they moved in order to quantify the components of the butterfly movements that contributed to the effectiveness of protean insurance. Using digitised movements of real animal models, with human participants tracking the movements in VR, I found that the passive movements of butterflies could be considered a form of protean insurance-based movement. To put this result into a wider context, the results of this chapter demonstrate that the detection of a predator by a prey item is not necessarily required in order to engage in protean movement. This finding provides an additional explanation for the function of the movement patterns of butterflies and other small diurnal swimming and flying animals.

3.2   Introduction

The ability of prey animals to detect predators forms an important selection pressure and is facilitated by many physiological and behavioural adaptations. For the former, this is most obviously represented by keen sensory capabilities (Dawson et al., 2004; Moir, Jackson, & Windmill, 2013; Wisenden, 2000; York & Bartol, 2014). For the latter, behaviours such as vigilance whilst foraging increase the chances of predator detection at the cost of reduced foraging efficiency (Brown, 1999; Lima, Valone, & Caraco, 1985). The successful detection of a predator allows the prey animals to deploy a variety of anti-predator defences and these may depend on the context of the predator-prey interaction. For example, if the predator has been detected after an attack has been initiated, the prey may engage in thanatosis (Miyatake et al., 2004) or startle displays (Martins, 1989; Umbers et al., 2017; Vallin, Jakobsson, & Wiklund, 2007). If the prey has been successfully captured, certain animals may utilise self-amputation (autotomy) whereby an animal sheds or discards one or more of its own appendages in order to elude a predator's grasp and escape (Congdon, Vitt, & King, 1974). Alternatively, if a predator has been detected, but has not initiated an attack, the prey item may engage in honest signalling (such as stotting [Stankowich & Coss, 2007] and alarm calls [Bergstrom & Lachmann, 2001]) to deter attacks. Additionally, a common response to all aforementioned contexts is for a prey item to flee from a predator (Edmunds, 1974).

However, in order to utilise many anti-predator adaptions effectively, the successful detection of a predator (in good time) is required. A common context within predator-prey interaction concerns when a prey item has been detected by a

predator, but the prey is still unaware of the predator's presence. This situation is most common in ambush predators, which conceal themselves and allow the prey to approach before a rapid attack (Carrier, Musick, & Heihaus, 2004). In a successful ambush, the prey item will be overwhelmed and rapidly incapacitated, thus preventing the employment of certain anti-predator adaptations (e.g. the ability to flee or the utilisation defensive structures). However, there is a specific context in which protean behaviour may offer an advantage to prey animals in this situation (i.e. the prey item is not aware of a stalking or intercepting predator), so called 'protean insurance'.

Protean insurance was first defined by Humphries & Driver (1970). The purported function of this behaviour is to offer an advantage to prey animals in situations where an attack is so rapid that any active avoidance action would be insufficient to prevent capture. Instead, frequent and unpredictable changes in their movement characteristics (for example, a sudden, tight turn) may interrupt targeting (a key determinant of successful predation; [Olberg, Worthington, & Venator, 2000]) or manoeuvre the prey item out of the way of an unseen stalking or intercepting predator (e.g. the predator may not be able to correct it's intercept trajectory following an unpredictable turn, thereby missing the intended target). Indeed, there are many examples of animals moving in erratic, seemingly protean movement patterns in situations where a predator has *not* been detected in free flights, black bean aphids (*Aphis fabae*) fly in an unstable manner, with their movements changing frequently, incorporating loops, criss-crossing and circling with fluctuating climb rates (Kennedy & Booth, 1963). Additionally, many species of small aquatic crustaceans are characterised by their jerking or weaving motions as they swim freely

(Colburn, Weeks, & Reed, 2007; Lewis, 1963; Paffenhöfer, Strickler, Lewis, & Richman, 1996). This movement type is perhaps most clearly displayed in larger insects such as butterflies, many of which display protean elements in their normal flight and simply exaggerate these elements upon detecting a predatory threat and attempting escape (Humphries & Driver, 1970). While the existence of protean insurance is commonly observed and taxonomically widespread (Humphries & Driver, 1970), there is little direct evidence supporting its efficacy in natural systems.

However, the study of the anti-predator benefits that putatively derive from protean insurance may overlap with other animal movement patterns that happen to result in unpredictable movements. Stochastic processes such as Brownian motion, random walks and Lévy flights are frequently used to model animal movements (Benhamou, 2007; Kareiva & Shigesada, 1983; Shlesinger & Klafter, 1986; Smouse et al., 2010). It is suggested that since stochastic processes such as Lévy flights can optimize search efficiencies, natural selection should have led to adaptations for Lévy flight foraging (Viswanathan, Raposo, & da Luz, 2008). These movements are intrinsically unpredictable and recent simulations have demonstrated that in certain contexts they can result in the evasion of prey items from predators (Abe & Kasada, 2020). It is therefore entirely plausible that protean insurance is in fact a coincidental benefit resulting from naturally selected stochastic foraging behaviour. While the key drivers behind protean insurance movements may be primarily derived from foraging selection pressures, these movements may nonetheless provide an anti-predator benefit in terms of evading predators, thereby conferring some selective benefit with respect to behavioural evolution and expression of foraging paths.

While understudied in nature, the strategy of protean insurance is well documented in military theory. One of the '10 commandments' for fighter pilots since the early 20th century has been to 'never fly straight and level in a combat zone for more than 30 seconds' (Barber, 2012). The purpose of this rule is twofold – firstly, to potentially evade unseen intercepting enemy aircraft and secondly, to reposition yourself to gain a different perspective of the surrounding area, and thereby view what were previously blind spots, from which enemy aircraft may have been approaching (Barber, 2012). The advantages conferred by this strategy reflect the purported benefits of protean insurance strategies in natural systems. However, while it is an intuitive assumption, only recently has the existence of this strategy in the animal kingdom been supported by some experimental evidence. Combes, Rundle, Iwasaki, & Crall (2012) found that fruit flies (*Drosophila melanogaster*) rarely respond to approaching dragonflies (*Libellula cyanea*) with evasive manoeuvres and were rarely successful when they did. This was primarily attributed to the outperformance of the dragonflies with respect to their flight characteristics in comparison to the fruit flies. However, random, erratic turns by the flies, (which occurred at similar frequencies whether the dragonfly predators were present or absent) were responsible for twice the amount of failed predation attempts than active evasive manoeuvres. This finding highlights a scenario where a protean insurance strategy can result in successful predator evasion, despite both a disparity between predator and prey with respect to flight performance and the lack of awareness of the prey with regards to an imminent predatory threat.

Due to the extremely limited experimental evidence available concerning protean insurance, I wished to examine flight movements of the painted lady

butterfly (*Vanessa cardui*) with respect to their efficacy as passive anti-predator behaviour (protean insurance). This model was chosen primarily due to the fact that they are considered one of the more conspicuous demonstrators of protean insurance in their normal flight (Humphries & Driver, 1970). By studying the qualities of their flight, and how these qualities affect the accuracy with which they can be targeted, I aim to explain how these protean flight sequences may reduce the ability of predators to target prey, specifically when the model animals are unaware of a predatory threat. In this study, I examined protean insurance movement using human 'predators' playing a 3D virtual reality (VR) simulation observing digitised flight paths of painted lady butterflies representing prey items. I hypothesised that specific qualities of the passive movements of butterflies could act as protean insurance-based movement, reducing the chances of capture by predators. In addition, I hypothesised that (similar to the digital animals of chapter two) the characteristics of butterfly flight paths would predict the overall effectiveness of the butterfly in terms of avoiding targeting by human participants. Specifically, I predicted that the most effective butterfly flight patterns (with respect to avoiding targeting) would consist of high speeds and high turning angles, indicative of protean insurance movements.

3.3   Methods

3.3.1   *Butterfly species selection, purchase, housing, maintenance and release*

The painted lady butterfly (*Vanessa cardui*) made a suitable model for a number of reasons. Most importantly, butterflies frequently display behaviour that is considered as protean insurance in flight (Humphries & Driver, 1970). The adult

butterflies are relatively large and therefore easy to extract trajectory data from videos of their flight. Furthermore, they are a well-studied species that is fast growing, native to the UK and readily available from suppliers. Butterfly larvae were purchased from Blades Biological Ltd. in June 2018. Larvae arrived in beakers containing a food/ water substrate for the larvae to feed upon in order to grow and eventually pupate. Upon pupation, individuals (n=40) were moved to 'bugdorm' enclosures (Height 0.7m, diameter 0.3m). The enclosures were supplied with wick feeders containing sugar/ water solutions (17 g sugar per 250ml water). Animals were housed in Minster House, University of Lincoln. Photoperiod was set at a 16 h light/ 8 h dark cycle. Temperature was maintained at ~20°C. All adults were tested within two weeks of emergence. Adults were released after testing as permitted by the University of Lincoln Research Ethics Policy. This project was approved by the College of Science ethics committee at the University of Lincoln (reference CoSREC265).

3.3.2   Butterfly flight recordings

Butterflies were placed onto a perch (H:1m) in the centre of a windowless testing room (approximate dimensions – H:3m, W:5m, L:6m) to fly freely. Flights were recorded using a Stereolabs 'ZED' camera connected to a windows PC running Microsoft Windows 10 (see Fig.3.1). This commercially available system utilises "passive stereo" with two cameras in fixed positions. As the images recorded from the left and right camera were a known distance apart, comparing the displacement of pixels between the two images allowed depth to be resolved (see following subsection). Recordings were made at 60 frames per second at a resolution of 720p.

The videos were also shot against a white background to reduce clutter, facilitating more precise trajectory extraction and to provide sharper contrast between the subject and the background. The videos were converted from their native format to AVI format via a lossless AVI codec using the Stereolabs SDK (Aymeric, Braun, & Yver, 2016). Recordings continued until 10 seconds of sustained, uninterrupted flight was recorded for each individual. Of the 80 filmed butterfly flights (two per individual), I chose one 10 second period of sustained flight for each individual, in which the butterfly was clearly visible and in motion for the entirety of the 10 second period. I also ensured the butterflies had been undisturbed for at least one minute post release. Due to the wide field of view of the cameras, and the depth of the room, butterflies typically remained in view for the entirety of their flights. This meant that the butterflies had been flying for approximately the same period of time for all selected 10 s periods of flight.
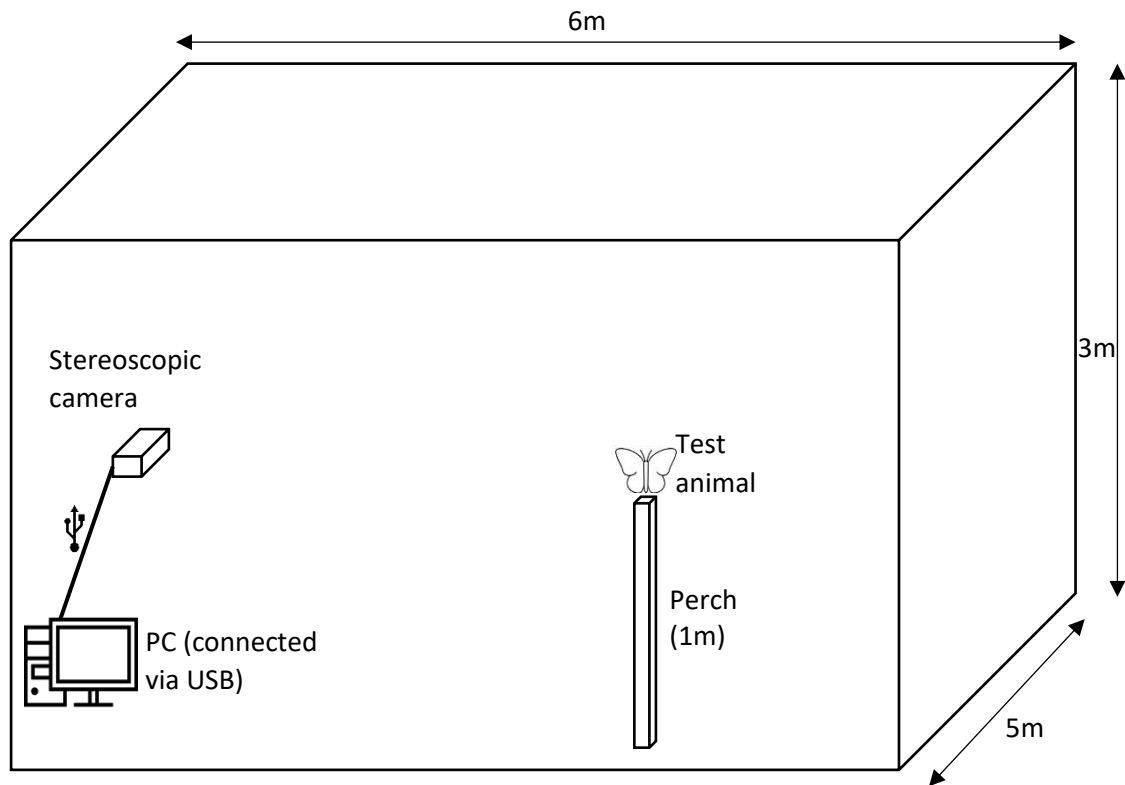
Fig. 3.1 Recording set up (not to scale)

3.3.3   Butterfly trajectory extraction

Trajectories of butterfly flights were extracted on a frame by frame basis using

MATLAB 2015. The AVI video clips featuring butterfly flights were loaded into

MATLAB and the pixel coordinates of the butterflies' positions (the approximate

centre of the visible pixels of the butterfly) were determined for each video frame

(left and right image). In order to calculate the distance from the camera for the

butterflies for each frame, the ZED camera was calibrated using the MATLAB Stereo

Camera Calibrator App (Computer Vision System Toolbox, MATLAB, 2015b). Using

the ZED camera (connected to a windows PC running Microsoft Windows 10), 20 still

images (PNG) were taken of a black and white checkerboard calibration target of

dimensions 297 x 420 mm (see Fig.3.2a). In all images, the calibration target was

presented fully within the field of view of both cameras, between one and six metres from the cameras and at an angle less than 45 degrees relative to the plane of the cameras. When the image pairs were added to MATLAB, the app used the images to produce a MATLAB 'stereoParams' object containing the intrinsic and extrinsic parameters of the camera and the distortion coefficients. The triangulate function (Computer Vision System Toolbox, MATLAB, 2015b) receives the stereoParams object and a matched pair of pixel coordinates (i.e. position data from the left and right camera of the relevant object) as inputs. The function then calculates the disparity between left and right pixel coordinates and takes into account the characteristics of the stereo camera. Finally, a set of cartesian coordinates are outputted that represent the position of the object in 3D.

The accuracy of the depth data extracted using this method was ground-truthed by using a laser rangefinder (Bosch™ DLR130K Laser Measure) to calculate the distance between the camera and a tripod mounted calibration target (see Fig.3.2b) set up at 90 positions throughout the flight area (varying heights and depths relative to the camera). Images of each position of the calibration target were recorded on the stereo camera. In all images, the calibration target was presented fully within the field of view of both cameras, between one and six metres from the cameras and directly facing the camera. The depth of the calibration target was then calculated using the triangulate function and compared to the laser rangefinder data to check the accuracy and precision of the MATLAB method (see Fig.3.3). A paired *t*-test showed no significant difference between the rangefinder data and the MATLAB calculated data ($t[88] = -0.43224$, $p = 0.66$). This indicated that there was no systemic error in the MATLAB method of extracting depth. Finally, a linear model was fitted to

the data with the MATLAB depth data predicting the laser rangefinder data. The MATLAB derived depth data significantly predicted the laser rangefinder data ($F_{1,87}$ = 4533.1, p < 0.001, R^2 = 0.98). The high adjusted r squared indicated a limited scatter around the fitted model and therefore high overall accuracy between the laser rangefinder data and the MATLAB depth extraction. I therefore extracted the butterfly trajectories using the stereoParams object and the triangulate function in MATBLAB.
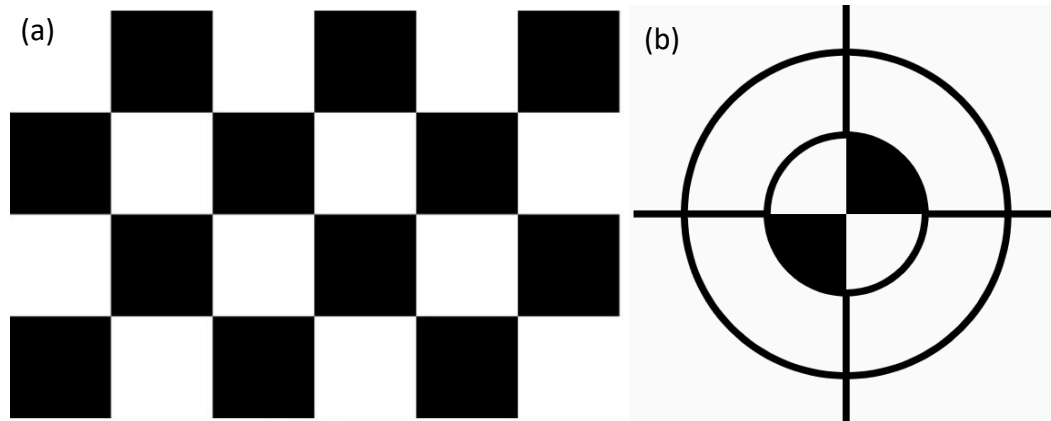
Fig. 3.3 (a) MATLAB Stereo camera calibration target (Computer Vision System Toolbox, MATLAB, 2015b). (b) Laser rangefinder calibration target

However, after extracting these trajectories, I noticed substantially more variation in the depth calculations (i.e. distance from the camera) in comparison to the lateral components of the trajectories (i.e. horizontal and vertical) than I had anticipated. This was most likely random error associated with the pixel extraction process due to the small body of the butterfly. As this depth error was in the same direction as the camera, this did not cause the overall trajectory of the butterfly to alter relative to a human participant observing the path in VR (see Simulations

below). Furthermore, the targeting metric was based on the arc distance to the object to reduce targeting error associated with changes in depth of the prey item (see Data collection below). However, the noise in the depth data could cause the VR object to 'flicker' as it moved back and forth rapidly relative to the observer. To account for this error, I performed another ground truthing calibration operation. I made 40 recordings involving moving a calibration target (see Fig.3.2b) along a metre rule. In all recordings, the conspicuous object was presented fully within the field of view of both cameras, between one and six metres from the cameras. The recordings were made at 40 positions throughout the flight area at varying heights, depths and orientations relative to the camera. I then extracted the cartesian coordinates of the calibration target trajectory. The depth error was also present in these trajectory data, however, since the trajectory was known (i.e. a 1 m straight line), I fitted moving average filters of various lengths until the cartesian coordinates resembled the known trajectories. The smallest filter that removed the majority of the depth error without misrepresenting changes in depth had a window of 30 frames (i.e. 15 frames leading and trailing the focal point), I then applied a filter of this size to the raw butterfly trajectory data (see Fig.3.4).
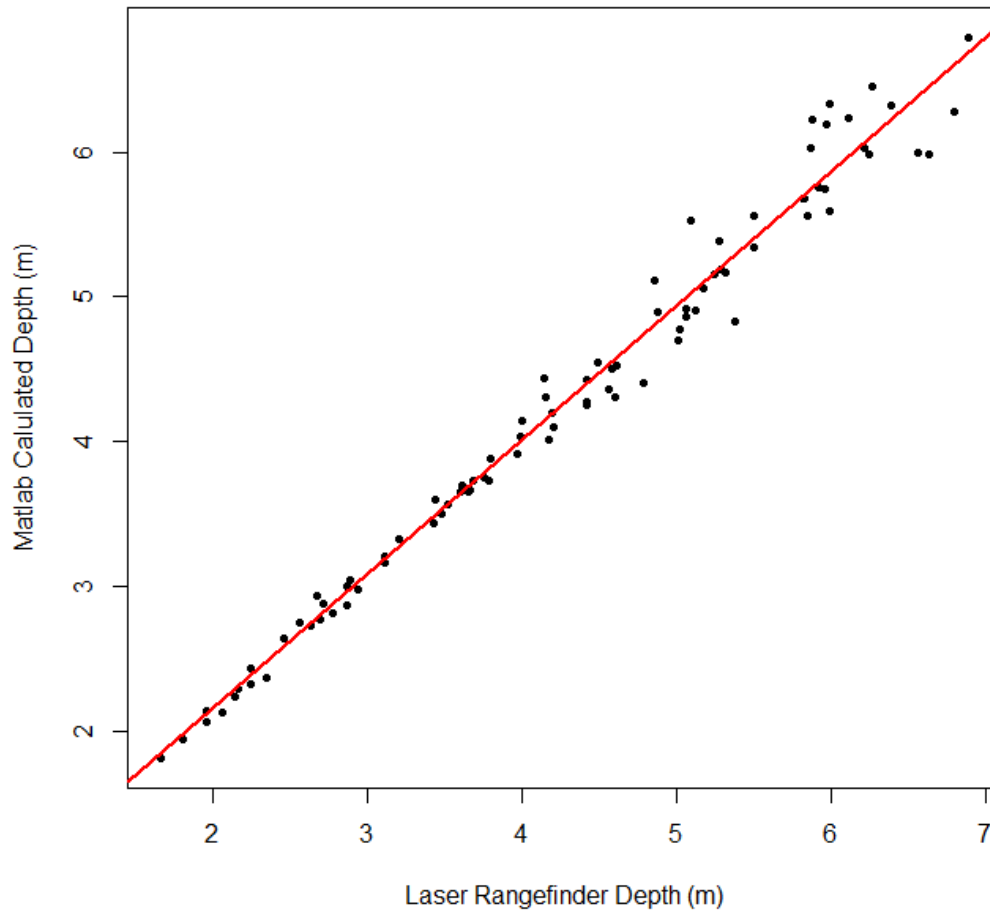
Fig. 3.4 Depth calculated using MATLAB triangulate function after stereo camera calibration (Computer Vision System Toolbox, MATLAB, 2015b) (x axis) against Laser rangefinder calibration target data

Unadjusted

(a)

Adjusted

(b)
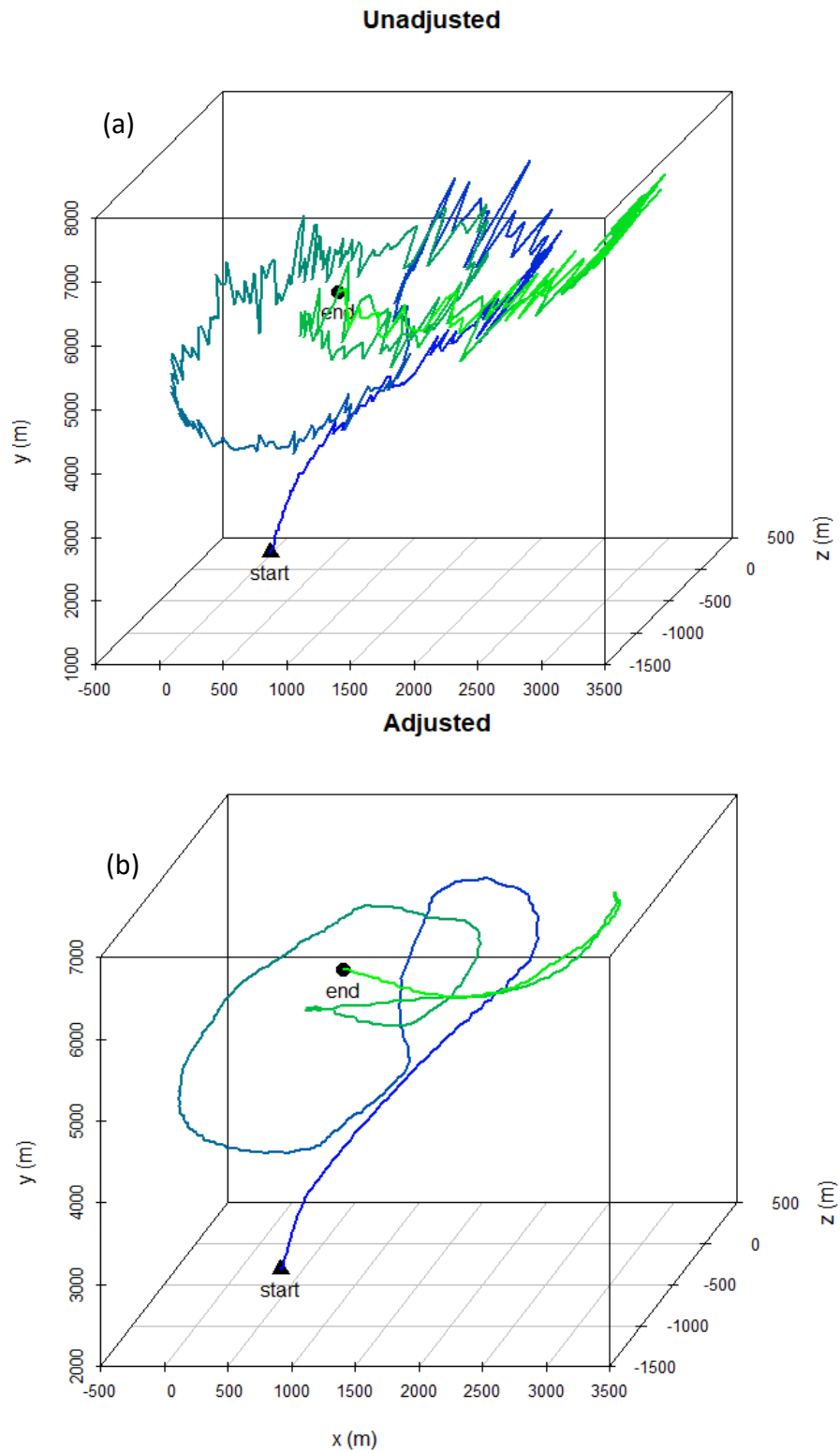
Fig. 3.6 (a) Selected example of a 3D movement trace of an unadjusted butterfly trajectory (b) The same 3D movement trace with an adjusted butterfly trajectory. The triangular points represent the starting positions while the circular points represent the ending positions.

3.3.4 Simulations

Simulation design, appearance and function was very similar to our previous study (see chapter two [Richardson, Dickinson, Burman, & Pike, 2018] for further methodological details). The fixed update function in the Samsung Gear VR system was used to display the frames at a consistent frame rate (50Hz), but the butterfly flight trajectories had been extracted at 60Hz. This required downsampling the trajectories from 60Hz to 50Hz and was done in MATLAB by fitting cubic splines to the x, y and z coordinates of trajectory data separately and resampling at the desired frame rate.

3.3.5 Experimental protocol

Human participants viewed the 40 extracted butterfly trajectories in VR. A total of n = 40 participants took part in this study (20 females and 20 males, with a mean age of 21.8 [range, 18 to 46]), all of whom were students of the University of Lincoln. Before providing consent to take part in the study, participants were given written information on the general aims of the study (although not the specific hypotheses being tested), what they would be asked to do, and the approximate time required to complete the study. Their age and gender were reported, but not linked to their experimental data.

The participants were instructed on the use of VR headset, including fitting and focus adjustment. As per the experimental protocol detailed in chapter two, participants were instructed that their task was to constantly target the prey item with the reticle as accurately as possible as it moved around the virtual environment. To start each trial, the participant used their head movements to position the reticle

over the black sphere representing the butterfly for one second. The butterfly trajectories were shown as they were recorded, so the sphere representing the butterfly would appear in varying positions within the participants front field of view. Once the participant indicated they were ready, experimental trials began. Each trial lasted 10 s and there were 40 experimental trials per participant. The order of experimental trials was randomized for each participant.

3.3.6 Data collection

Telemetry data of the participant's head orientation (a 3D vector passing through a point between the participant's eyes and towards the reticle) were collected every 0.02 s throughout each trial. As the depth error had been reduced but not eliminated entirely, I considered targeting in terms of the arc distance (radians) between the participants gaze and the position of prey items. This was because, unlike the distance between the participants gaze and the prey centre, arc distance would not change based on increased depth of the prey item with respect to the human participant.

I then used the data on prey location to compute a measure of overall butterfly movement path complexity, using the information-theoretic approach detailed by Herbert-Read et al. (2015). This method quantifies the complexity of a signal. Chapter two demonstrated that when applied to 3D movement traces, entropy is a significant predictor of human performance (see chapter two for further details regarding the application of this technique to 3D movement traces).

Additionally, I calculated the grand means of speed and turn angle for all butterfly flight paths (i.e. the mean speed and turn angle of all butterfly flight paths

combined). I then categorised the speed and turn angle of each flight path as either 'high' or 'low' by determining whether the mean speed and mean turn angle of each individual flight path sat above (high) or below (low) the corresponding grand means. This decision provided continuity between the first data chapter (which also included categorical variables for components of movement) and the real animal data collected here, while also allowing direct comparison.

Finally, I calculated which individual portions of butterfly flights were the most effective in terms of avoiding accurate targeting by human participants. As each flight path was seen 40 times (by the 40 human participants), I calculated a mean targeting distance for each frame for every path. From these values, I then calculated a grand mean and standard deviation for targeting distance. Any frame of movement where the mean targeting distance was greater than two standard deviations from the grand mean was categorised as 'good performance' with respect to the butterfly (unintentionally) evading human targeting. All other frames were categorised as 'poor performance'.

3.3.7 Statistical analysis

All analyses were conducted using generalised linear mixed-effect models (glmm) in R version 3.3.2, using the lmer and glmer functions (for linear mixed models and logistic regression, respectively) in the lme4 package (Bates et al., 2015). I first tested whether path complexity predicted targeting accuracy, regardless of the movement characteristics of underpinning each flight path. Log_{10}-transformed targeting accuracy was included as the dependent variable, with path complexity as a continuous predictor and trial order as a covariate to control for possible learning or

fatigue effects over consecutive trials. Each participant's anonymous identifier was included as a random effect to control for repeated data from the same individual human participant. I also included the path identity as a random effect to control for the repeated exposure of each movement path (i.e. each participant saw the same 40 movement paths in experimental trials). In all models, significance was determined by comparing the full model to a reduced model lacking the term of interest using a likelihood ratio test (Crawley, 2005). The validity of the model assumptions was confirmed by visually assessing the normality of the model residuals.

Next, I considered whether the characteristics of the butterfly flights (specifically the speed and the turn angle) predicted participant performance. Each model included $\log_{10}$-transformed targeting accuracy as the dependent variable, and the categorisation of each flight characteristic (i.e. speed: high/ low; turn angle: high/ low), as fixed factors. I included the same covariates and random effects as the previous model. An interaction was also fitted between the fixed factors.

Finally, I wanted to examine what made the butterflies most difficult to track on a frame by frame basis, rather than the summarised characteristics of an entire path. To that end, I fitted a logistic regression. The regression included butterfly performance for each frame (in this case, 'good performance' for butterfly frames were ones and poor performance frames were zeros) as the dependent variable, and the speed and turn angle values for that frame, as continuous predictors. Path identity and the frame number were included as random effects. An interaction was

also fitted between the continuous predictors. Full model outputs for all analyses are included in Appendix A.

3.4 Results

Flight characteristics varied substantially throughout individual flight paths. Fig.3.5 visualises both a time series of these changes and a frequency analysis of the flight characteristics.
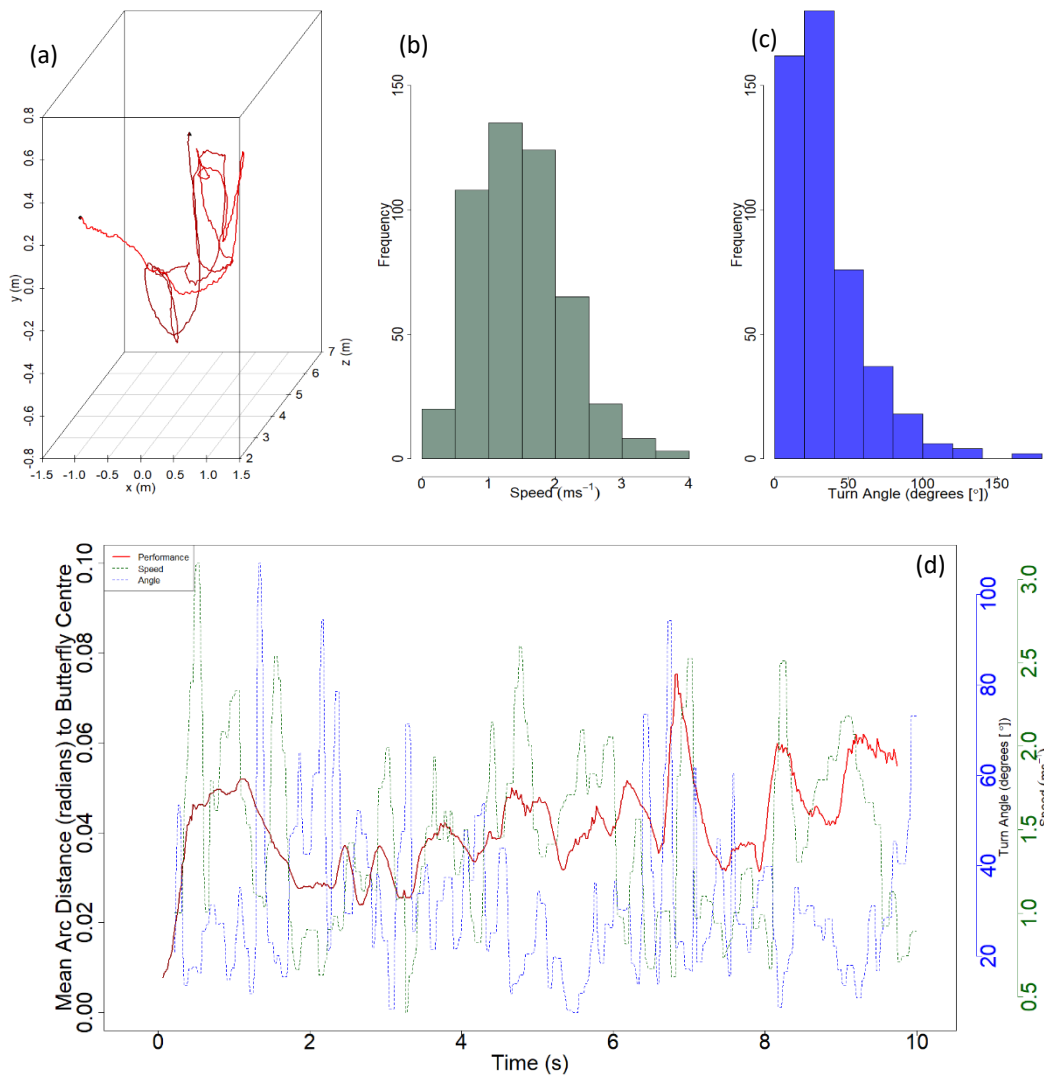
Fig. 3.8 (a) 3D movement trace representing an example flight path. The triangular point represents the starting position, while the circular point represents the ending position. (b) frequency histogram of the speed characteristics (ms^{-1}) recorded by the example flight path. (c) frequency histogram of the turn angle (°) characteristics recorded by the example flight path. (d) time series of the example flight path. The red line represents the mean arc distance (radians) of human participants' gaze to the centre of the prey item throughout the 10 s example flight path. The green and blue dotted lines represent the speed and turn angle time series respectively. Note the secondary and tertiary y axes on the right. The colour of each axis (green and blue) correspond to speed (ms^{-1}) and angle (°) values respectively.

3.4.1   Does butterfly flight path entropy predict human performance?

In line with my prediction and similar to chapter two, I found that entropy (a measure of path complexity) predicted participant performance (χ^2_1 = 9.04, $p < 0.001$; Fig.3.6). Specifically, as entropy increased (i.e. movement paths became more complex), participant performance worsened (i.e. participants tracked butterflies less
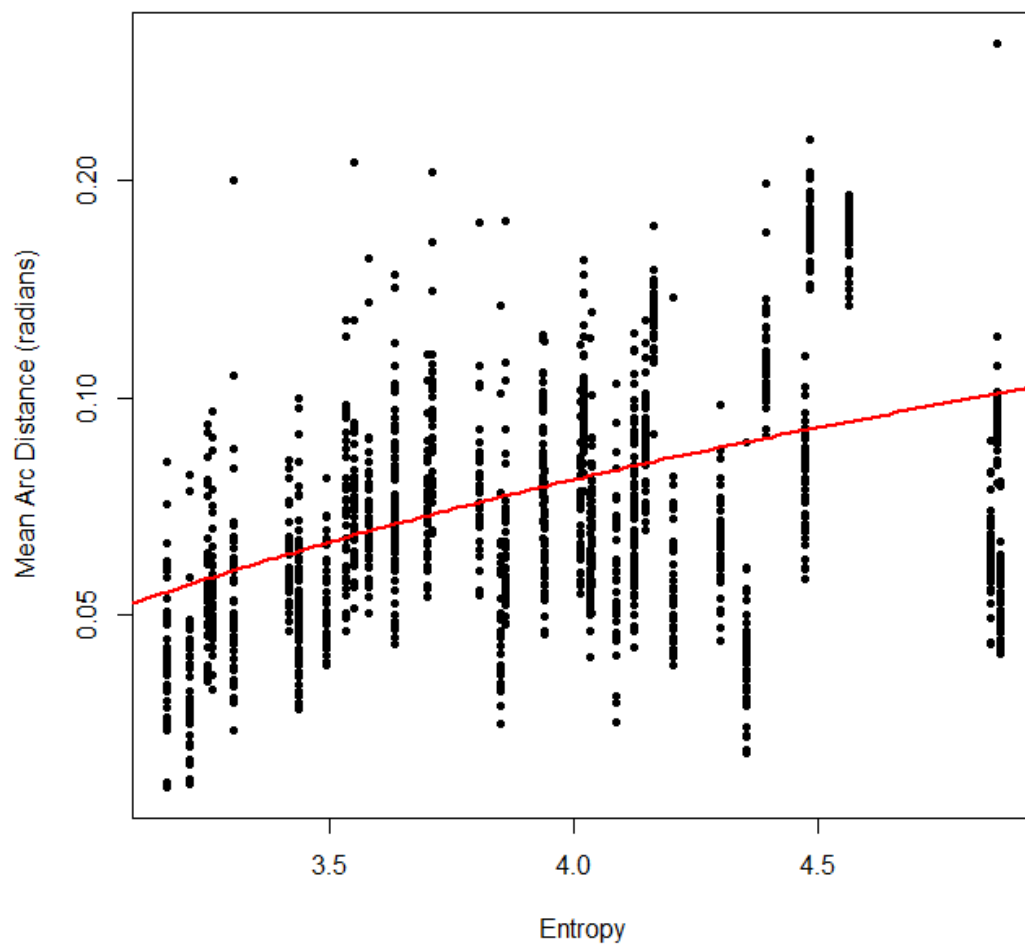
Fig. 3.9 Targeting accuracy (measured as the arc distance [radians] from the centre of the prey item over each trial) as a function of movement path complexity. Higher values along the x-axis denote more complex movement segments, while higher values along the y-axis denote poorer targeting accuracy. Note the log scale on the y-axis. The red line denotes an lmer model fit.

accurately).
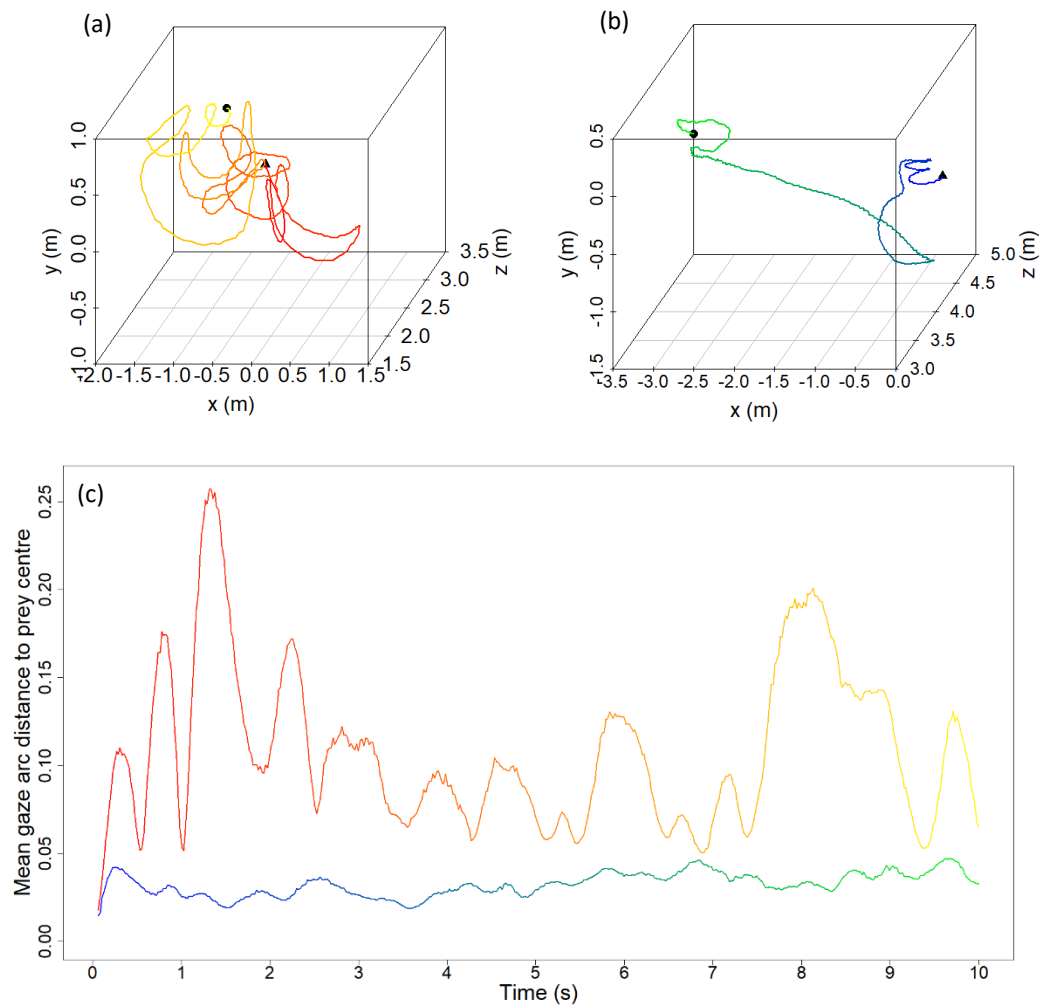
Fig. 3.11 (a, b) 3D movement traces of the best and worst performing butterfly movement paths respectively. The triangular points represent the starting positions while the circular points represent the ending positions. Note that both figures represent the same area of space (a box of dimensions w:3.5m, h:2m, d:2m). (c) a time series representing the mean distances of human participants' gaze to the centre of the prey item throughout each 10 s movement path. Note that the colour of the time series matches the movement trace to visualise where peaks and troughs of performance occurred. Finally, note that both time series constitute 10 s of movement, therefore the most effective path was moving at a much higher overall speed as evidence by the movement trace.

3.4.2   Do overall butterfly flight characteristics predict human performance?

Fig.3.7 visualises the differences in participant performance between different butterfly flight paths. When examining the effects of butterfly movement path characteristics on human participant performance, the interaction was non-significant and was therefore removed from the model. Indeed, I found that only

speed significantly predicted participant performance (χ_1^2 = 7.83, *p* = 0.01; Fig.3.8). Specifically, faster butterflies moving with higher mean speeds were targeted with significantly lower accuracy (i.e. having a greater mean distance from the prey's centre) than butterflies moving with slower mean speeds.
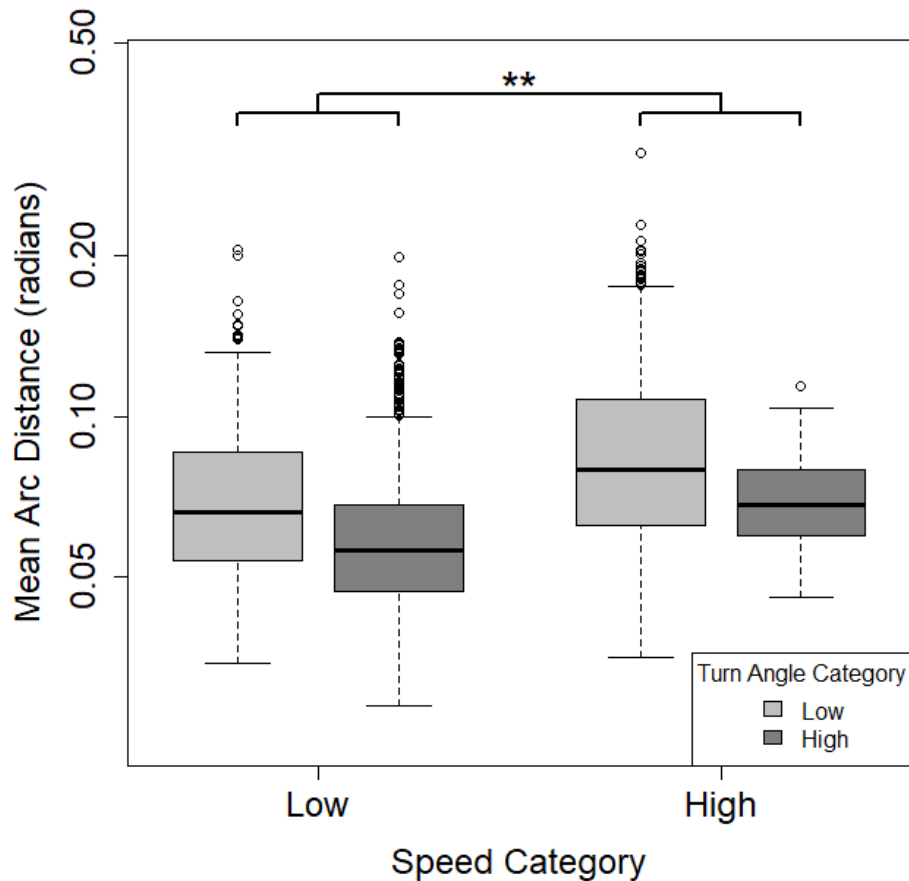
Fig. 3.12 Targeting accuracy (measured as the arc distance [radians] from the centre of the prey item over each trial) as a function of movement path characteristics. Higher values along the y-axis denote poorer targeting accuracy. Note the log scale on the y-axis. Asterisks denote significant differences (**, p < 0.01) between categories.

3.4.3   What characterises the most effective butterfly movements on a finer temporal scale?

Fig.3.9 shows an example butterfly flight that includes a period of particularly effective movement patterns. Fig.3.10 shows frequency histograms from the same

flight comparing characteristics between good and poor performance of the butterfly (with respect to human targeting).
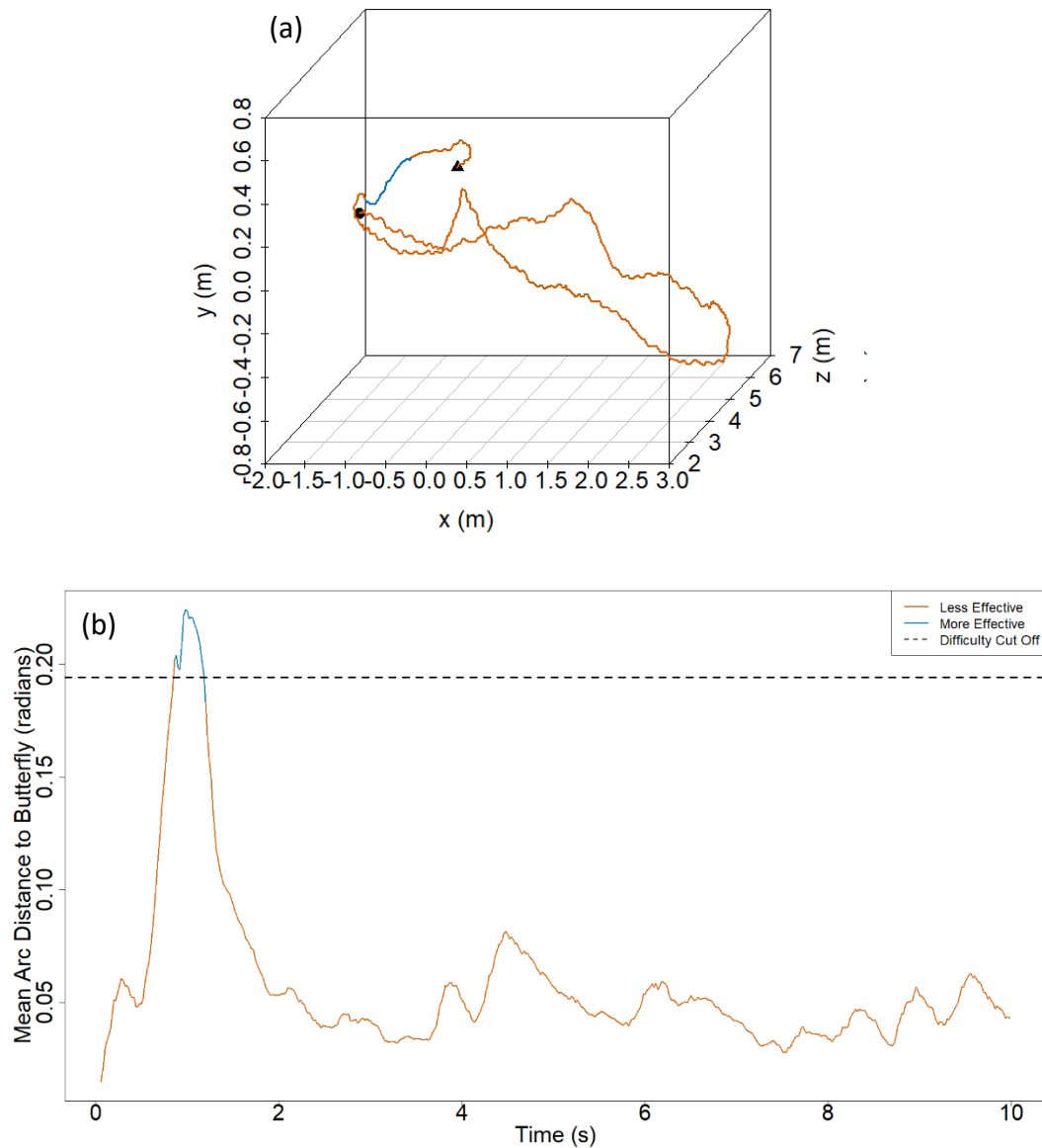
Fig. 3.15 (a) 3D movement trace of an example flight path. The blue portion of the movement trace represents a period of 'good performance' from the butterfly with respect to evading human targeting (i.e. the mean arc distance of participants targeting the object during this period was greater than two standard deviations from the mean), while orange represents 'poor performance'. The triangular point represents the starting position while the circular point represents the ending position. (b) a time series representing the mean arc distances of all 40 human participants' gaze to the centre of the prey item throughout the 10 s example movement path. Note that the colour of the time series matches the movement trace to visualise where the difficult performance occurred. The dotted black line represents the difficulty cut-off.
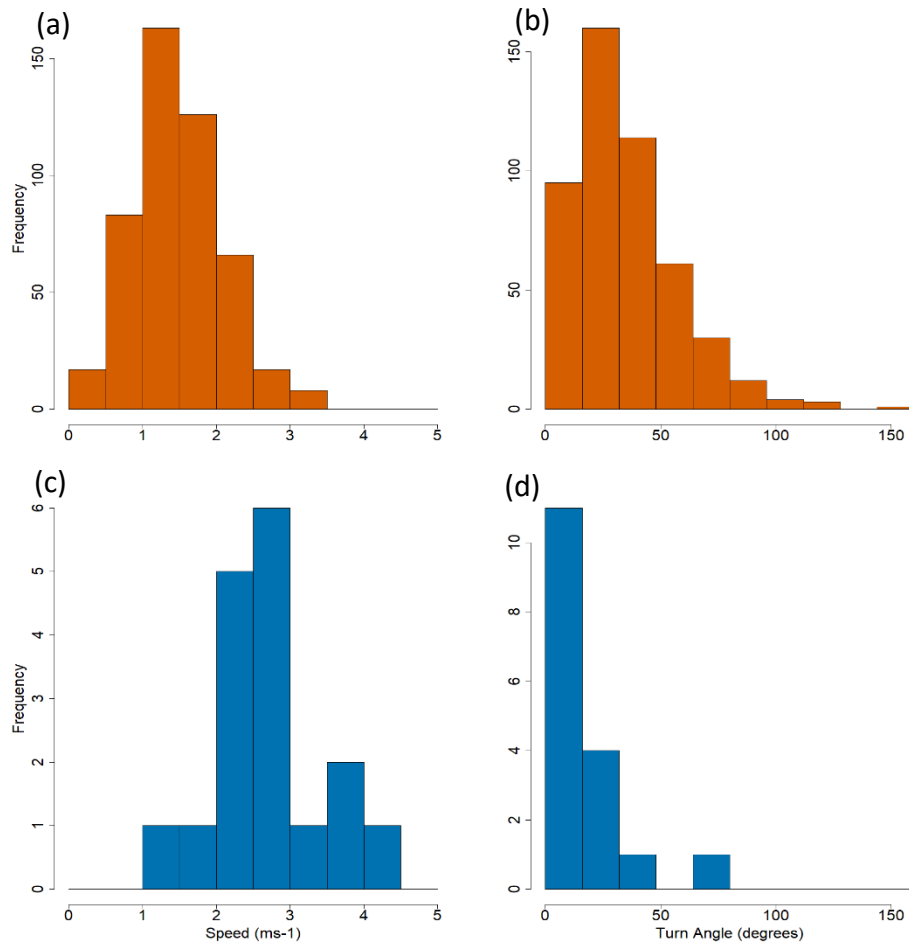
Fig. 3.18 Frequency histograms of the flight characteristics for the example path featured in Fig.3.8. (a) poor performance speed distribution. (b) poor performance turn angle distribution. (c) good performance speed distribution. (d) good performance turn angle distribution. Note that the distributions are colour-coded as with Fig.3.9.

When examining the flight characteristics of particularly effective parts of butterfly flight in terms of participant targeting accuracy (i.e. having a greater distance between the participant's gaze and the prey's centre) in comparison to less effective sequences, I found that speed and turn angle significantly predicted participant accuracy (speed: $\chi^2_1 = 49.54$, $p < 0.001$; turn angle: $\chi^2_1 = 10.39$, $p = 0.001$; Fig.3.11). Specifically, the butterfly movements that were targeted with the least accuracy consisted of faster speeds ($z = 6.84$, df = 19875, $p < 0.001$) and narrower turning angles $z = -3.25$, df = 19875, $p < 0.001$).
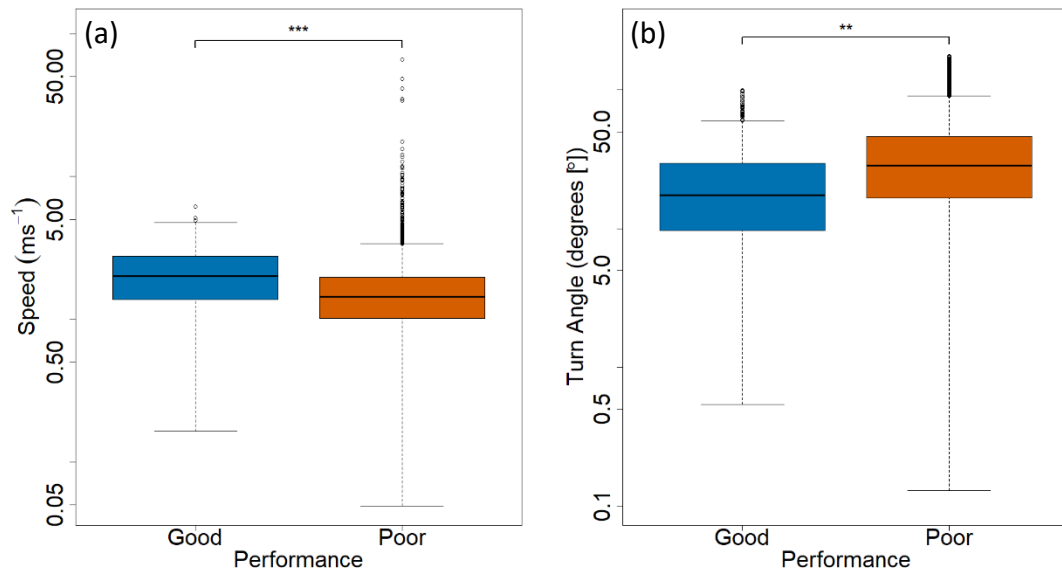
Fig. 3.23 (a) boxplot comparing good (blue) and poor (orange) performance values for all speed characteristics (in metres per second). Asterisks denote significant differences (***, p < 0.001) between categories. (b) boxplot comparing good (green) and poor (red) performance values for all turn angle (in degrees) characteristics. Note the log scale on both the y-axes. Asterisks denote significant differences (**, p = 0.001) between categories.

3.5 Discussion

In this study I have shown that in a real animal model, increasing mathematical complexity of butterfly movement paths resulted in more difficult movement paths with respect to targeting difficulty. Furthermore, when examining the flight characteristics of entire butterfly movement paths, I found that only speed (and not turning angle) significantly predicted targeting difficulty. However, when I examined the butterfly movement paths on a finer temporal scale, I found the most effective butterfly movements were significantly predicted by higher speeds and lower turning angles, though there was no interaction between the two. Butterflies are considered to be among the most conspicuous demonstrators of protean insurance movement (Humphries & Driver, 1970). Here I have examined the components of their movement paths that make them more difficult to target, both in terms of their

overall path characteristics, and the fine scale components that result in poor targeting by human participants acting as predators. These findings supported my overall hypothesis that the passive movements of butterflies incorporate protean elements that could be considered a form of protean insurance-based movement. Contrary to my prediction however, the most effective protean insurance movement paths did not consist of high turn angles and high speeds, but high speeds and low turning angles. The results presented here lead to the inference that certain movement patterns displayed by the model animals could confer an increase in survivability without detection of a predatory threat.

When looking at the movement paths on the finer temporal scale, the relationship between lower turning angles and more effective protean movement (in terms of poorer targeting accuracy for human predators) was an unexpected result, as was the non-significant interaction between turning angle and speed, particularly as these two factors tend to be related in animal locomotion (Wilson et al., 2015). I believe that a plausible explanation for this relationship is contextual and due to the distance of the target from the human predators. Sharp turning angles provide a greater chance of evasion when the predator is closer (i.e. about to intercept) (Combes et al., 2012). However, sharper turns result in deceleration as a result of conservation of angular momentum. From a moderate or long distance, substantial slowdowns resulting from sharper turns may result in easier targeting due to the lower efficacy of evasive turns from distance and subsequent lower speed.

Previous studies have found that prey exhibit increased movement path complexity following a simulated threat (Herbert-Read et al., 2017; Schaerf et al.,

2017). In this study, no direct predatory threat (simulated or otherwise) was present, yet increasing complexity still significantly predicted increasing difficulty for predators with respect to targeting a prey item. Most butterflies show erratic protean movements in their free flight and it has been suggested that active protean movements in response to a predator are simply exaggerated forms of their protean insurance movement paths (Humphries & Driver, 1970). Whereas the digital prey items in chapter two could be imbued with whatever properties of movement desired, the movement characteristics of real animals are constrained by physical limitations. For example, in general for flying animals, as body mass increases, so too does speed at the cost of reduced manoeuvrability (Ellington, 1991). When comparing butterfly flights to human performance, speed has been shown to be the largest single component in terms of predicting targeting difficulty. This seems to be consistent whether examining the characteristics of an entire 10 second flight path, or examining particularly difficult sections of butterfly movement on a frame by frame basis. However, even for animals with a relatively low body mass, the energetic investment for faster flying is considerable. Furthermore, lower speeds allow for greater manoeuvrability due to reduced inertia (Hedrick & Biewener, 2007). Rapid erratic turns have been demonstrated to be effective in a slightly different protean insurance context to that presented here (i.e. when a predator has intercepted a prey item and is within striking range [Combes et al., 2012]). The presence of sharp turns in the butterfly movement traces (see Figs. 3.3b, 3.4a, 3.6a,b, 3.8a), while not effective at evading human predators from a moderate distance as demonstrated here, may aid in the evasion of unseen intercepting predators about to strike (*sensu* Combes et al., 2012). By incorporating both types of movements (i.e. high speeds and

occasional sharp turns) animals moving with protean insurance may interrupt the targeting of more distant predators (via high speeds) and increase the chances of evasion from unseen intercepting predators about to strike (via occasional sharp turns). This suggests that, there are both real world energetic considerations animals must make, and contextual benefits to moving at lower speeds with greater manoeuvrability (Domenici, Blagburn, & Bacon, 2011; Howland, 1974; McLachlan, Ladle, & Crompton, 2003).

The study by Combes et al. (2012) suggests that while protean insurance may offer a chance of evasion while in-flight, the overall likelihood of evasion is still fairly slim. For many prey species there may be more effective and/or less costly behaviours that could reduce their chances of capture by an unseen stalking predator. Indeed, purported protean insurance behaviour is generally observed under the following (fairly narrow) set of criteria (see Humphries & Driver, 1970 for greater detail):

1. They spend considerable periods of time free-swimming or free-flying and are therefore more conspicuous to predators as there are fewer environmental elements to break line of sight in comparison to terrestrial or benthic animals.

2. They are relatively small, which typically results in a large range of potential predator species (Cohen et al., 1993), many of which may outperform them with respect to their sensory capabilities (i.e. more able to detect the prey without its knowledge) and/ or flight characteristics (i.e. size, speed, agility etc.).

3. They are primarily active during daylight hours, increasing the likelihood of detection.

4. There is a strong, sustained predation pressure on the population.

Due to the narrow range of circumstances that are conducive to the expression of protean insurance, the selection pressures that favour the development of protean insurance may be relatively weak compared to more acute selection pressures that can result in the expression of complicated movement paths on a similar scale to purported protean insurance movements, for example, foraging paths. Animal foraging paths are often unpredictable and can be represented by stochastic processes such as Lévy flights (Benhamou, 2007; Shlesinger & Klafter, 1986). These processes may be subject to selection pressure (Smouse et al., 2010). If optimal foraging paths are adaptive and selected for, and as a result of their intrinsic unpredictability, also reduce the chances of targeting as the evidence presented here indicates, it may be that the coincidental benefits of increased chances of evading unseen predators (brought about by their unpredictable nature) further increase the selection pressure in favour of increasing complexity and/ or unpredictability of animal foraging pathways. It may therefore be the case that the behaviour described as protean insurance, while effective in its purported role in anti-predator defence, is linked (or entirely subsumed by) to the evolution of behaviours such as foraging paths.

Due to the nature of this study, there are several limitations regarding the interpretations that can be drawn. Firstly, as the movements of real animals were used as opposed to digital representations of real animal movements (as in all other

studies within this thesis), physical laws of flight are in effect. These include effects such as inertia and gravity (the latter assists dives [powered or otherwise] and slows climbing). For simplicity in determining the fundamental characteristics that contribute the efficacy of protean movement patterns, these effects are not simulated in other studies. As a result, the movement traces that the human participants observed in this study differ compared to all other studies in this thesis and therefore limit the direct comparisons that can be made between this study and others contained within this document. The most notable difference is the relatively higher speeds (and consequent increased efficacy) that are resultant from powered or unpowered gravity assisted dives. Additionally, while a lower body mass of the model animal means that the inertia is reduced (e.g. allowing more rapid acceleration and tighter turns), they are of course, still in effect affect the flight capabilities of the insects (Lenz, Chechkin, & Klages, 2013). To elaborate, unlike other studies in this thesis, speed and turn angle are not entirely independent of one another. This is particularly expressed at high speeds. The observed relationship between high speeds and low turning angles (resulting in the most effective protean insurance sequences) is therefore likely resultant of high speeds (which were the strongest individual predictor of poor targeting by human predators both here, and in chapter two) reducing the ability of the butterfly to turn, as opposed to the narrow turning angles actually assisting with evading targeting. Furthermore, while there were no active predatory threats to the butterflies, the perception of a threat may remain. While practical steps were taken where possible to encourage 'passive' protean movements in flight (these steps included the experimenter leaving the room once the fight was released and ensuring at least one minute of free flight had occurred

movement trajectories extraction), it cannot be stated with certainty that the selected flight trajectories are representative of truly passive protean movement. For example, the novelty of the testing environment, or olfactory cues from the experimenter that remained after leaving the room may have been perceived as predatory threats requiring active evasion by the test animals. Finally, while human participants agreed to target the digital prey to their best ability, it cannot be guaranteed they were doing so at all times, due to distraction, disorientation, disinterest etc. Despite these limitations, several general conclusions can be drawn about the study.

In summary, this study elucidates the characteristics of the butterfly flights (frequent demonstrators of protean insurance movement) that enhance evasion of targeting by human predators when under no direct threat of predation. Specifically, when looking at the characteristics of entire flight paths, increasing path complexity and increasing speed significantly predicted poorer performance for human participants with respect to targeting butterflies. Additionally, when examining the most effective butterfly movement sequences in terms of avoiding predatory targeting on a finer temporal scale, I found that increasing speed and lower turn angles significantly predicted poorer targeting performance. To put the results of this study into a broader context, here I have provided experimental support for the widely held assumption that passive animal movement patterns can constitute a protean insurance strategy that can reduce chances of capture by undetected predators. I have also included an explanation for the general pattern of protean insurance movements and explored reasons for the occurrence of this strategy in nature. Finally, the comparable findings between the digital animals used in chapter

two and the real animal movements examined here further demonstrates the utility of the virtual methodology in the study of the adaptive behaviour. Having examined protean behaviour in two different contexts with both digital prey and using a real animal system, I next wanted to examine the effects of group dynamics on protean movement, in particular, how the size of an animal grouping affected the difficulty of targeting protean prey items. This is the subject of chapter four.

4. Chapter 4: Group Size and Anti-Predator Movement

4.1 Chapter Abstract

Animal groupings are extremely common in nature and the benefits and drawbacks to individuals within animal groupings are generally well studied. An influential phenomenon within animals groupings (with respect to the ability of predators to capture prey items) is the 'confusion effect' where the presence and movement of many individuals within a grouping of prey animals causes an overloading of the predator's visual analysis channel, resulting in reduced capture rates. Furthermore, protean movement of an individual has been shown to reduce the chances of capture by a predator. It is uncertain whether these two anti-predator phenomena are able to interact in groupings of prey items (thereby affecting the ability of predators to capture individual prey items within groupings). This data chapter utilised two approaches (a controlled experiment and a citizen science project) to examine this question from different perspectives. The results of both studies showed no significant interaction between group size and the mathematical complexity (an indicator of protean movement efficacy) of uncoordinated protean movements. The results of this study are of particular interesting given the equivocal findings of previous studies examining this question.

4.2 Introduction

The formation of groups shown by many animal species is a commonly observed and well-studied phenomenon. There are numerous costs and benefits associated with group living for animals. Examples of costs include increased disease and parasite

transmission rates (Alexander, 1974) and intraspecific resource competition (Ward & Webster, 2016). Examples of benefits include increased mating opportunities (and overall higher quality offspring) (Ward & Webster, 2016) and increased foraging efficiency (Rubenstein, 1978). However, among the most influential factors resulting in the formation and maintenance of animal groups is considered to be the reduced risk of predation for grouped individuals via 'safety in numbers' (Lehtonen & Jaatinen, 2016).

The term 'safety in numbers' is a broad term that typically refers to the resultant effects of anti-predator phenomena associated with gregariousness in animals. There are many mechanisms by which grouped individuals may provide reduced chances of capture by predators. These mechanisms are diverse, closely interlinked, and may interact with one another to produce further benefits to groups of organisms (Lehtonen & Jaatinen, 2016). Examples include the dilution effect which refers to the reduced risk of capture for an individual prey item by a predator by virtue of the increased number of available targets (Foster & Treherne, 1981). Another example is 'selfish herding' behaviour, where individuals under a predatory threat are continuously attempting to adjust their location with respect to the grouping to a (perceived) safer position (or attempting to maintain that position). When predators attack from outside of the group (as is most common [Hamilton, 1971]), the safest position is typically in the centre of the group, far from the peripheral, where risk of capture is greater (Hamilton, 1971). As a final example, the "confusion effect" describes the reduced attack-to-kill ratio experienced by a predator resulting from an inability to single out and attack an individual prey in a group (Krakauer, 1995).

The confusion effect is perhaps most frequently observed in shoaling fish (Pitcher, 1986) and flocking birds (Carere et al., 2009). A confusion effect can occur when the presence and movement of many individuals within a grouping of prey animals causes an overloading of the predator's visual analysis channel (Broadbent, 1965) resulting in an information processing bottleneck for the predator. This in turn can result in less successful predation (i.e. more attacks per capture as group size increases) (Landeau & Terborgh, 1986; Penry-Williams, Ioannou, & Taylor, 2018). While evidence suggests that the confusion effect manifests more readily when prey movement is coordinated (i.e. individuals move towards near neighbours and align their travel directions) (Ioannou et al., 2012), confusion effects can occur even in small groups with simple, uncoordinated movements of prey items (Ruxton, Jackson, & Tosh, 2007). In addition to the study of the confusion effect in animal systems, the confusion effect has been studied numerous times in human psychology, typically via visual search tasks (see Tosh, Krause, & Ruxton, 2009 for review) and has led to the use of human subjects in experiments investigating the confusion effect from a biological perspective (e.g. Hogan, Hildenbrandt, Scott-Samuel, Cuthill, & Hemelrijk, 2017; Jones et al., 2011; Ruxton et al., 2007; Scott-Samuel et al., 2015). While these group effects can reduce the chances of capture, it has also been shown that elements of an individual's movement (e.g. the speed and variation in turning angles [Richardson et al., 2018]) can predict the ease or difficulty with which a predator is likely to have in capturing prey items.

When an individual animal is targeted by a predator, if it perceives the predatory threat, there are a variety of anti-predator behaviours that it can engage in. A common response is to utilise protean movement. Anecdotal examples of

protean movement often note the increasing unpredictability of the movement patterns compared to normal movement as the primary driver reducing the ability of predators with respect to capturing the prey item (Driver & Humphries, 1988; Humphries & Driver, 1970). This increase in unpredictability by animals responding to a threatening stimulus has been quantified in studies such as Herbert-read et al. (2015), who demonstrated that movement path complexity (entropy) of Pacific blue-eyes (*Pseudomugil signifer*) increased in response to a stimulus representing a predatory threat. Chapters two and three provided direct evidence that increased complexity (entropy) of protean movements predicted poorer accuracy of human participants when attempting to target digital items representing prey. These findings demonstrated that in both movements simulating animal behaviour and digital representations of real animal movement, the information entropy has been an effective, general predictor of targeting difficulty. Furthermore, groups of prey items can induce a confusion effect and the strength of this effect increases based on the number of individuals in the group (Jeschke & Tollrian, 2007; Miller, 1922). This is a well-established phenomenon, however, less well understood is the interaction between increasing protean movement efficacy (e.g. increased movement path complexity) and the increase in the confusion effect resultant from a greater number of individuals. Specifically, do increasingly protean movements and an increasing confusion effect interact with one another to result in a further increase in targeting difficulty for predators? Existing studies into this question have reached conflicting conclusions.

Jones, Jackson, & Ruxton (2011) used varying group sizes of 'protean' and 'predictable' black digital prey items on a computer screen (white background). All

prey items moved at the same speed, with the same rules for turning frequency (i.e. turns were more likely as the prey items moved away from the centre), but protean prey items had larger variance in potential turning angles and therefore moved more unpredictably. They found that the advantages of protean versus more predictable movements were independent of group size, and therefore protean behaviour did not enhance the confusion effect as they had initially predicted. A later study by Scott-Samuel, Holmes, Baddeley, & Cuthill (2015) used small textured squares, the colouration of which was made up of three shades of grey (referred to as trinary noise squares) representing prey items on a background consisting of the same trinary noise texture as the prey items (i.e. the prey and background were matching). The study also examined the interaction between group size, prey density and movement path unpredictability. Similar to Jones et al.'s (2011) study, the only movement factor that varied between more and less predictable groups was the turning angle variance (although six levels of turn angle variance in random walks were used to create movement paths). In contrast to Jones et al.'s (2011) result, Scott-Samuel et al. (2015) reported a confusion effect at higher path unpredictability values that significantly interacted with prey density to predict poorer targeting for human participants. These examples highlight the uncertainty regarding the interaction between the confusion effect and movement path complexity. It is also worth noting that in addition to the differences in visual presentation of stimuli, there were further differences between the studies by Scott-Samuel et al. (2015) and Jones et al. (2011) which may explain the differing findings. Firstly, the nature of the task for the human participant and therefore the quantification of the effectiveness of prey movements with respect to evading human predators differed. Scott-Samuel et

al. (2015) had human participants target and track a chosen prey item via mouse movements whereas Jones et al. (2011) had human participants 'capture' prey via mouse clicks. Furthermore, the qualities of movement differed between the studies. Jones et al. (2011) manipulated turning angle in prey items which swarmed around the centre of the screen, whereas Scott-Samuel et al. (2015) manipulated the predictability of movement for items which performed random walks whilst constrained by the screen boundaries.

Studies investigating group dependent effects have utilised the number of individuals present (i.e. group size) and/ or the area occupied by the target items divided by the arena size (i.e. group density). While these two metric are different, they are not truly independent. Altering the group size increases the group density to the observer. The only way to maintain group density and increase group size would be to proportionally decrease the size of the prey items as group size increased. In this study, I wished to maintain consistency with respect to the size of the prey items from the perspective of the observer. I therefore chose to consider group in terms of size as opposed to density. While I consider group density an inappropriate metric for this study, the non-independence of the two metrics means that literature examples that utilised group density are still relevant to this study and as a result are included for comparisons and discussions.

This chapter details two studies that examined the relationship between protean movement effectiveness (using entropy as a general predictor of protean movement efficacy) and the confusion effect induced by the number of individuals in a group. Each study used VR to investigate this question, but utilised variant

approaches. The first study (hereafter referred to as 'local') consisted of a controlled study with a similar experimental design to those described in earlier chapters. The second study (hereafter referred to as 'citizen science') consisted of a 'gamified' VR simulation that utilised a citizen science approach developed and distributed via Steam. In addition to aesthetic differences between the local and citizen science experiments, the measure by which prey movement effectiveness was quantified also differed. The local study used a targeting method based on gaze as with earlier chapters, which is comparable to the targeting method used by Scott-samuel, Holmes, Baddeley, & Cuthill (2015). The citizen science study utilised an active capture method representative of animals that can use their tongues as ballistic projectiles to capture prey (i.e. chameleon). This approach was comparable to the active capturing of prey items in (Jones et al., 2011). While the methods used by both Scott-Samuel et al. (2015) and Jones et al. (2011) are commonly used to represent animal movements (e.g. Dobbinson et al., 2020; Hall et al., 2013; Tosh et al., 2006), variation in all qualities of movement (i.e. speed, turn angle and the time between turns) allows more realistic representation of animals movements, for example, when engaging in swarming behaviours and protean movement. Furthermore, swarming or shoaling behaviours are associated with free-flying or free-swimming animal groupings and the use of VR facilitates a more realistic representation of these movements, primarily through the resolution of depth. The key hypothesis of this study is that there would be a significant interaction between the size of a group of protean prey items and their movement path complexity that would affect the ability of human predators to target or capture prey items. Specifically, in parts of this study, I predicted that prey items would be targeted or captured less effectively by human

participants as group size and movement complexity rose. Regarding the nature of the interaction, I predicted that rising values of group size and movement complexity would interact to result in an additional increase in the overall difficulty of capture. If this hypothesis is supported, it would align more with the findings of Scott-Samuel et al. (2015) rather than Jones et al. (2011) and indicate that the beneficial confusion effect associated with groupings of uncoordinated prey items is dependent on the qualities of the movement patterns of individuals within groupings and specifically, can be enhanced by more effective protean movements.

4.3 Materials & Methods

4.3.1 Experiment 1: local data collection

4.3.1.1 Simulations

Similar to chapter two (Richardson et al., 2018), all simulations were created in the Unity3D game engine running on a Microsoft Windows PC, and built to run on a Samsung Galaxy S7 smartphone using the Samsung Gear VR system.

Simulations consisted of a number of black spheres functioning as 'prey' (either one, five or ten individuals) presented against a homogenous white background to maximise contrast. The prey moved in a 3D virtual space centred on a point 30 m directly in front of the participant. The prey items moved within a spherical area with a diameter of 20 m. Prey items therefore subtended a maximum visual angle of 0.1 radians and a minimum of 0.02 radians. Within the simulation, participants were free to look around the virtual environment. A small, red circle (the reticle) was superimposed onto the centre of the participant's field of view and provided a point of reference for the participant to facilitate targeting, allowing them

to interact with moving prey items in real time. The dimensions of this 'flight area' facilitated the simulation of a grouping of animals (i.e. swarming insects such as midges) and ensured prey movement stayed within a comfortable range of motion for all participants with respect to their head movements. This had two primary benefits. First, it kept all individuals within the participant's field of view, so all individuals were visible to the participant at all times in experimental trials. Secondly, it allowed us to isolate protean movement efficacy in terms of head movements alone, rather than a combination of head movements and the noise introduced by the reorientation of participants' bodies to target objects that have moved outside of their comfortable range of motion.

Prey movement used similar principles to the prey items in chapter two, namely a series of steps during each of which it travelled in a straight line in 3D space before turning and moving off on a different trajectory. Movement of prey in the simulation was determined by three parameters: the speed at which the prey moves within the virtual environment in metres per second (hereafter referred to as 'speed'), the angle in degrees turned within a cone centred on the prey's direction of travel (hereafter termed 'angle') and the time in seconds until the next turn (hereafter termed 'time'). Regarding the final value, in the first data chapter, a set distance was reached before a turn was executed. In this study and all subsequent studies, a timer was used to call turns as it was functionally identical to a distance variable but easier to implement when using probability mass functions to draw the characteristics of flight paths (see below).

Prey movement values (speed, angle and time) were decided based on a combination of real animal data and pilot studies. The search space of the speed parameter was decided using an animal speed database (see Hirt, Jetz, Rall, & Brose, 2017 [supplementary material]). I calculated the 95th percentile of this speed data as our upper limit. This was done in order to eliminate some of the extreme max speed values, which primarily consisted of birds of prey in powered dives as opposed to sustained level flight and were therefore slightly misleading. This resulted in a maximum speed value of 26.16 ms^{-1}, with our speed range being between 0 ms^{-1} and 26.16 ms^{-1}. For the time characteristic, the maximum value was decided based on the amount of time it would take a prey item moving at max speed to get from the centre of the flight area to the edge of it. The lower value was based on the fixed update function in the Samsung Gear VR system was used to display the frames at a consistent frame rate (50Hz). This put the range of time values from 0.02 s to 0.38 s. Finally, the angle search space was based on values obtained from pilot experiments and constrained the widest possible turn to 0.25 π radians, thereby putting the range of angle values between 0 radians ± 0.25 π radians (see following paragraph for clarification). Prey movement paths could then be drawn from these distributions. These paths were represented by a series of Cartesian coordinates in 3D space saved to individual text files which could be read and displayed by the VR system.

Using these flight characteristics, I generated digital 'genotypes' which consisted of probability mass functions (PMF) for the aforementioned three parameters. Discrete uniform distributions between two randomly generated values within each parameter search space were generated. 'Low' complexity genotypes featured a single discrete uniform distribution. The complexity of a genotype could

be increased by generating multiple discrete distributions, which were then summed and normalised to create one PMF (genotype) (see Fig.4.1). This is how higher complexity genotypes were generated. Specifically, 'moderate' complexity genotypes consisted of two discrete uniform distributions (summed and normalised to create one PMF), while 'high' complexity genotypes consisted of five discrete uniform distributions (summed and normalised to create one PMF). It is worth noting that while speed and time characteristics were represented by a single range of values, turn angle was represented in spherical coordinates (azimuth and elevation), so the PMF's consisted of two ranges representing azimuth and elevation (see Fig. 4.5c for further clarification). I found that these values of genotype complexity resulted in flight paths that showed clear and consistent variation in the appearance of flight paths between complexity levels. Furthermore, the generated flight paths from each genotype complexity level were significantly different from one another. Specifically, after calculating the entropy values for every 10 s flight path that was seen by participants (n = 1920), Welch's two sample t-tests (with Bonferroni adjustment) showed that mean entropy scores for each complexity level were significantly different from one another, and that expressed path complexity increased as genotype complexity increased (Low complexity – high complexity: t[3367.1] = -13.39, p < 0.001; low complexity – moderate complexity: t[2556.9] = -19.79, p < 0.001; moderate complexity – high complexity: t[3181.7] = -6.64, p < 0.001). Additionally, the spread of entropy values decreased as genotype complexity increased (see Fig.4.1). To clarify, these analyses were conducted to demonstrate the differences in entropy values between genotype levels. Entropy is not used in subsequent analyses in this part of the chapter. This was because calculating the

entropy value of a path would represent a sampling of a genotype, whereas genotype

distributions are representative of the entirety of the data. Subsequent analyses have

therefore used the genotype data instead of individual flight path data.
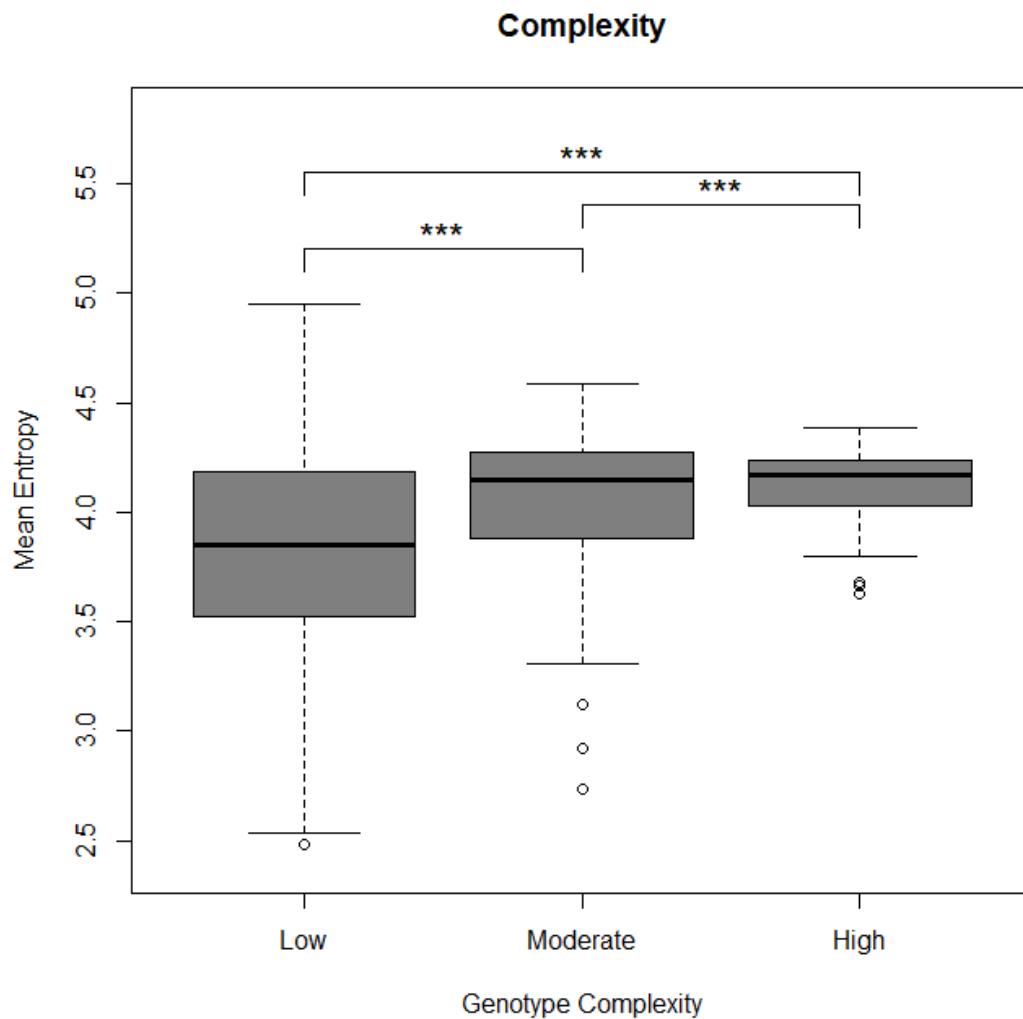
Fig. 4.1 Boxplot displaying the differences in mean entropy scores generated from genotypes that were displayed to participants. Asterisks represent significant differences (*** = p < 0.001). Note that spread of entropy values decreases as genotype complexity increases. Also note that this figure is purely to demonstrate the differences in entropy values between genotype levels. Entropy is not used in subsequent analyses in this part of the chapter.

To produce flight paths from a genotype, firstly, a starting position was randomly generated within the flight area. Secondly, the initial speed, angle and time were randomly selected from the genotype. Then, the trajectory of a prey item moving according those values was recorded in Cartesian coordinates and added to a text file. When the time value was reached (i.e. the number of frames corresponding to the initial time value in seconds), new values of speed, turn angle and time until turn were drawn from the genotype. This process continued until either

1. The trajectory passed out of the flight area, whereupon the trajectory would be adjusted, specifically by drawing new values from the genotype until the path trajectory was within the bounds of the flight area.

2. Ten seconds of trajectory data had been generated, whereupon the text file containing the path coordinates was saved.
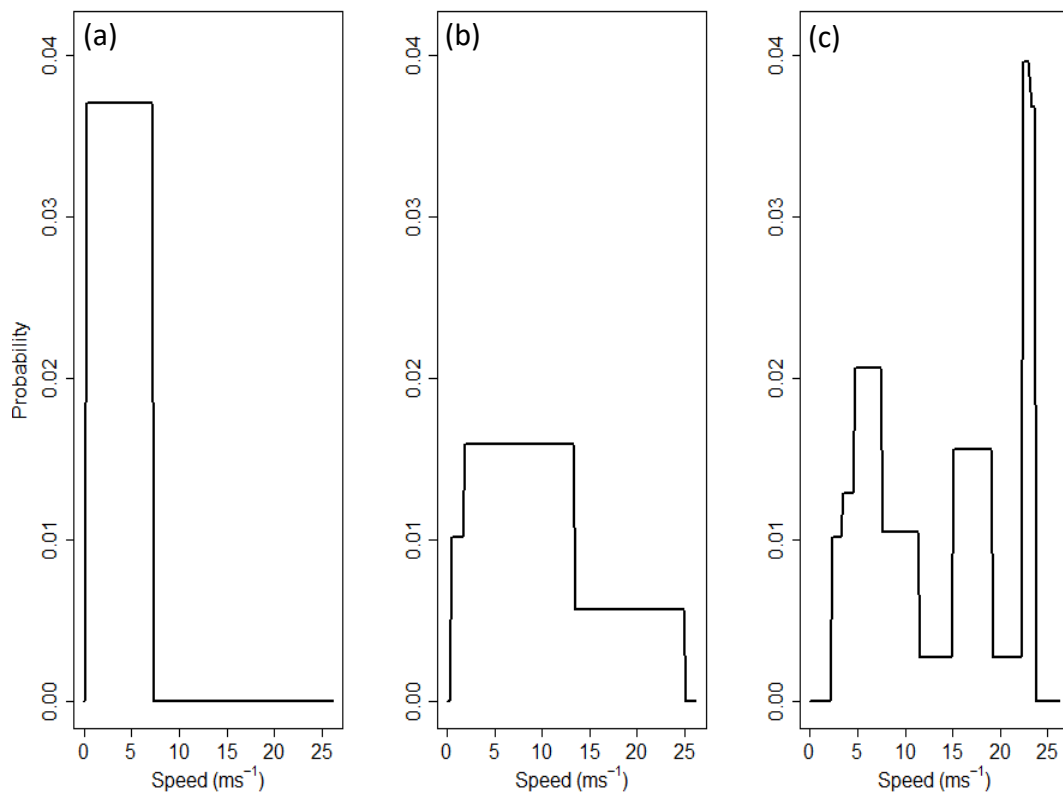
Fig. 4.5 Example speed distributions for the three different complexity levels. Low (a), moderate (b) and high (c). Density sums to one. Note the increasing complexity between the figures (left to right).

The confusion effect is predicted to occur even when group sizes are small (less than ten individuals) (Krakauer, 1995; Tosh et al., 2006). Furthermore, Krakauer (1995) predicted that the incremental benefit (through increased confusion) of adding individuals to the group declines with increasing group size. In order to more clearly quantify the effects of a greater number of individuals on human performance, I utilised relatively small group sizes in this study, namely groups of one, five and ten individuals.

4.3.1.2   Experimental protocol

A total of *n* = 40 participants took part in this study (23 females, 17 males; mean age = 23.8 [range, 19 – 45]), all of whom were staff or students at the University of Lincoln. Before providing consent to take part in the study, participants were given written information on the general aims of the study (although not the specific hypotheses being tested), what they would be asked to do, and the approximate time required to complete the study. Their age and gender were reported, but not linked to their experimental data. This project was approved by the College of Science ethics committee at the University of Lincoln (reference CoSREC265). After consent was given, a detailed verbal briefing was given to each participant to ensure they understood their role in the data collection.

Participants saw 30 trials in total (3 training trials, followed by 27 experimental trials). Each participant saw all combinations of genotype complexity and group size (nine combinations, see table 4.1). Furthermore, all participants saw three separate genotype sets (i.e. three independent low, moderate and high complexity genotypes), thereby resulting in 27 experimental trials. Participants put on the headset and familiarised themselves with the VR environment. Once the participant indicated they were ready, the experimenter began the simulation, starting with the three training trials. The three training trials consisted of one, five and ten individuals, respectively. The prey item(s) would begin moving (after a three second visual countdown indicator) according to low complexity 'training genotypes'. This was done so the participant could familiarise themselves with the VR environment and acclimate to displays of multiple objects. Once the training trials

were completed, if the participant indicated they were not comfortable targeting a single prey item from a group, three more training trials were conducted. The experimental trials only began when participants indicated they were ready. Each trial presented the participant with a number of prey items that were positioned and orientated within the flight area according to the starting points of the flight paths (text files) that had been generated from their genotypes. After a three second visual countdown indicator, the prey items would begin moving according to their flight paths. For all trials, each participant was instructed that they were to choose any single prey item and target it as accurately as they could. In this case, accurate targeting referred to maintaining the targeting reticle on the centre of the chosen prey item (or as close to the centre of the chosen prey item as they were able) via their head movements. Furthermore, participants were instructed that they were free to change the object they were targeting at any time, for any reason. The only condition was that they were always attempting to target a prey item as accurately as possible throughout each experimental trial. The order of the experimental trials was randomised for each participant.

Table 4.1 Breakdown of experimental treatments. Each participant saw movement paths from all nine permutations of genotype complexity and group size. Furthermore, each participant saw three sets of unique genotypes, resulting in 27 experimental trials in total.

Genotype Complexity	Number of Individuals		
	1	5	10
Low	1/ Low	5/ Low	10/ Low
Moderate	1/ Moderate	5/ Moderate	10/ Moderate
High	1/ High	5/ High	10/ High

4.3.1.3   Data collection

Telemetry data of the participant's head orientation (a 3D vector passing through a point between the participant's eyes and towards the reticle) were collected every 0.02 s throughout each trial (this method of telemetry recording was used in chapters two and three [also see Richardson et al., 2018]).

Due to the multiple prey items in view in each trial, using the distance between the participants gaze and the prey item to quantify which object was being targeted was somewhat ambiguous in the presence of multiple prey items. For example, if a human participant was targeting a relatively distant prey item, a nearer prey item may be closer the human participants gaze when considering the Euclidian distance between the two (or vice versa). I therefore sought a metric to more accurately determine the likelihood of which object was being targeted. In order to do so, I conducted a pilot experiment where multiple objects were presented to a human participant, but only one specified prey item was consistently targeted. I then compared the accuracy of two targeting metrics with respect to correctly identifying which prey item was being targeted via a paired *t*-test. The first was the Euclidian distance between the nearest point along a participant's gaze and the centre of the prey item (as used in chapter two). The second was the arc distance in radians between the participants gaze and the centre of the prey item (as used in chapter three). Specifically, I created a VR simulation with ten prey items, one of which was coloured red (the 'focal' prey item), while the remaining nine were black. 40 genotypes of 'moderate' complexity (see experimental protocol, above) were generated and for each genotype, 10 movement paths were drawn to create 40 trials

consisting of ten individuals. The flight characteristics and flight area were the same as in the experimental protocol. In each trial, the human participant attempted to accurately target the focal prey item consistently. The Euclidian distance and arc distance between the participants gaze and each of the 10 prey items was calculated for each frame of each trial. For each trial, the number of frames that each targeting metric correctly identified the focal prey item as the one being targeted was recorded (see Fig.4.3). A paired *t*-test showed a significant difference between the arc distance targeting metric and the euclidian distance targeting metric ($t[77.59] = -4.454$, $p < 0.001$). The arc distance showed that the focal prey item was correctly identified as the object being targeted with a higher degree of accuracy when multiple prey items were present. This metric was therefore used in to identify which object was being targeted in experimental trials.
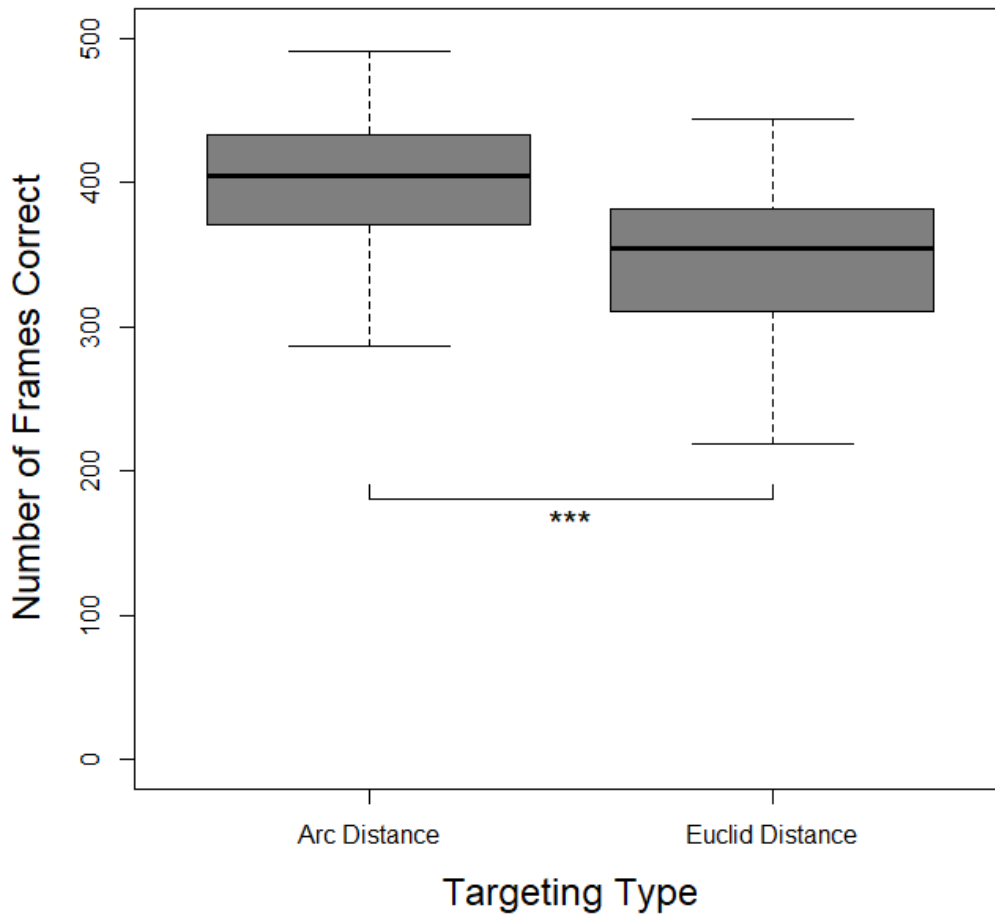
Fig. 4.7 Boxplot displaying the number of frames the focal prey item was correctly targeted in pilot studies depending on the targeting metric used. Note that each trial was 10 seconds (500 frames at 50Hz) long. Asterisks denote significant difference ($p < 0.001$) between categories.

For data collected from experimental trials, I used both the human predator gaze data and the prey position data to calculate the arc distance in radians between the participants gaze and the nearest object (which was considered the one being targeted) for each frame. However, when increased numbers of individuals were present, there were more opportunities for prey items to (for example) pass in front of the actual targeted prey item. The occluding prey item may thereby have a

narrower arc distance than the targeted prey item, giving the false impression that it is the object being targeted. This resulted in the narrower arc distance being recorded when the targeted item was in fact a greater arc distance away. While this was an infrequent occurrence, the chances of this type of error occurring increased as the number of prey items present increased. I therefore introduced a control to account for this confound. I calculated the arc distances between a 'control' gaze (a static gaze vector [0,0,1] pointing from the participants head position to the centre of the prey flight area) and the prey items for each frame of each trial. This control value would be smaller as the number of prey items increased. I then subtracted the mean of this control arc distance for each trial from the mean arc distance between the human participant and the nearest prey item for each trial to obtain an adjusted targeting distance. This value represented targeting accuracy while compensating for the varying number of prey items present in each trial.

4.3.1.4   Statistical analysis

All analyses were conducted using general linear mixed-effects models (glmm) in R version 3.5.2, using the lmer function in the lme4 package (Bates et al., 2015). The validity of the model assumptions was confirmed by visually assessing the normality of the model residuals. I tested whether complexity and group size predicted prey targeting accuracy. I included participant's targeting accuracy (adjusted arc distance in radians) as the dependent variable. The number of individuals present in each trial and the genotype complexity where used as categorical predictors and an interaction was fitted between these two terms. I included trial order as a covariate in order to control for possible learning or fatigue effects over consecutive trials. I also included

each participant's anonymous identifier as a covariate to control for varying aptitudes for object targeting between participants. Finally, I included the genotype identifier as a random effect to control for repeated viewings of each genotype. To elaborate, while each participant saw unique genotypes, every genotype was used to derive paths for the three categories corresponding to the number of individuals present (i.e. one, five and ten individuals). Significance was determined by comparing the full model to a reduced model lacking the term of interest using a likelihood ratio test (Crawley, 2005). Full model outputs for all analyses are included in Appendix A.

4.3.2 *Experiment 2: citizen science*

4.3.2.1 Simulations

The FlyCatcher game was created in the Unity3D game engine running on a Microsoft Windows PC, and built to run on the HTC Vive, Oculus Rift and Steam VR systems. The use of the game to collect data from the general public required separate ethical approval. An application to use the game to collect data from the general public was submitted via the Lincoln Ethics Application System and was subsequently approved by the College of Science ethics committee at the University of Lincoln (application reference 2019-Feb-0157). The game was released on the video game digital distribution service 'Steam' on the 6th Nov 2019. A number of concessions were made regarding the game in order to increase playability and consequently, engagement by the general public. Firstly, as opposed to the black prey items presented against a white background (as with all other experimental VR simulations detailed in this thesis), a more visually appealing environment was used (see Fig.4.4b) and the prey items were represented by animated 3d models of flies (see Fig.4.4a). Additionally,

rather than targeting prey items purely via gaze, the participant attempted to capture prey items by directing their head movements toward a prey item and pressing a button, whereupon a 'tongue' object would extrude and 'capture' the prey if the tongue and a prey item collided. This was representative of certain predators which can use their tongues as ballistic projectiles to capture prey items (i.e. chameleon, frog, certain salamander sp.). If a prey item was captured, it was removed from the scene. The tongue extended and retracted in the space of one second and only one prey item could be caught per button press. Players were encouraged to create profiles to distinguish between different individuals playing the game on the same device.

Prey items moved in a 3D flight area that was centred on a point 2 m directly in front of the participant with a radius of 1.25 m. Prey items subtended a maximum visual angle of 0.06 radians and a minimum of 0.02 radians. The dimensions of this 'flight area' facilitated the simulation of a grouping of animals (i.e. swarming insects such as midges) and ensured prey movement stayed within a comfortable range of motion for all participants with respect to their head movements.

Prey movement path generation followed the same principle as experiment one. I aimed to replicate the movements of an animal that is associated with both swarming and protean movement. I chose blowflies which meet both criteria (Jander, 1975; Ma et al., 2012). The study by Bomphrey, Walker, & Taylor (2009) consisted of precise measurements of the typical flight performance of the blowfly *Calliphora vicina* in free flight. Prey movement values (speed, angle and time between turns) were therefore based on the information gleaned from this study. The search space

of the speed parameter was based on the typical values of flies in free flight between

and therefore set to 1.2 and 2.5 ms^{-1}. The maximum turn rate of the flies was found

to be 30 radians s^{-1}, When scaled to the 50Hz framerate used here, that resulted in a

maximum turn angle of $\pi/5$ radians. The angle search space was therefore between

0 radians and $\pi/5$ radians. For the time characteristic, the maximum value was

decided based on the amount of time it would take a prey item moving at max speed

to get from the centre of the flight area to the edge of it. The lower value was based

on the fixed update function to display the frames at a consistent frame rate (50Hz).

This put the range of time values from 0.02 s to 1.66 s.
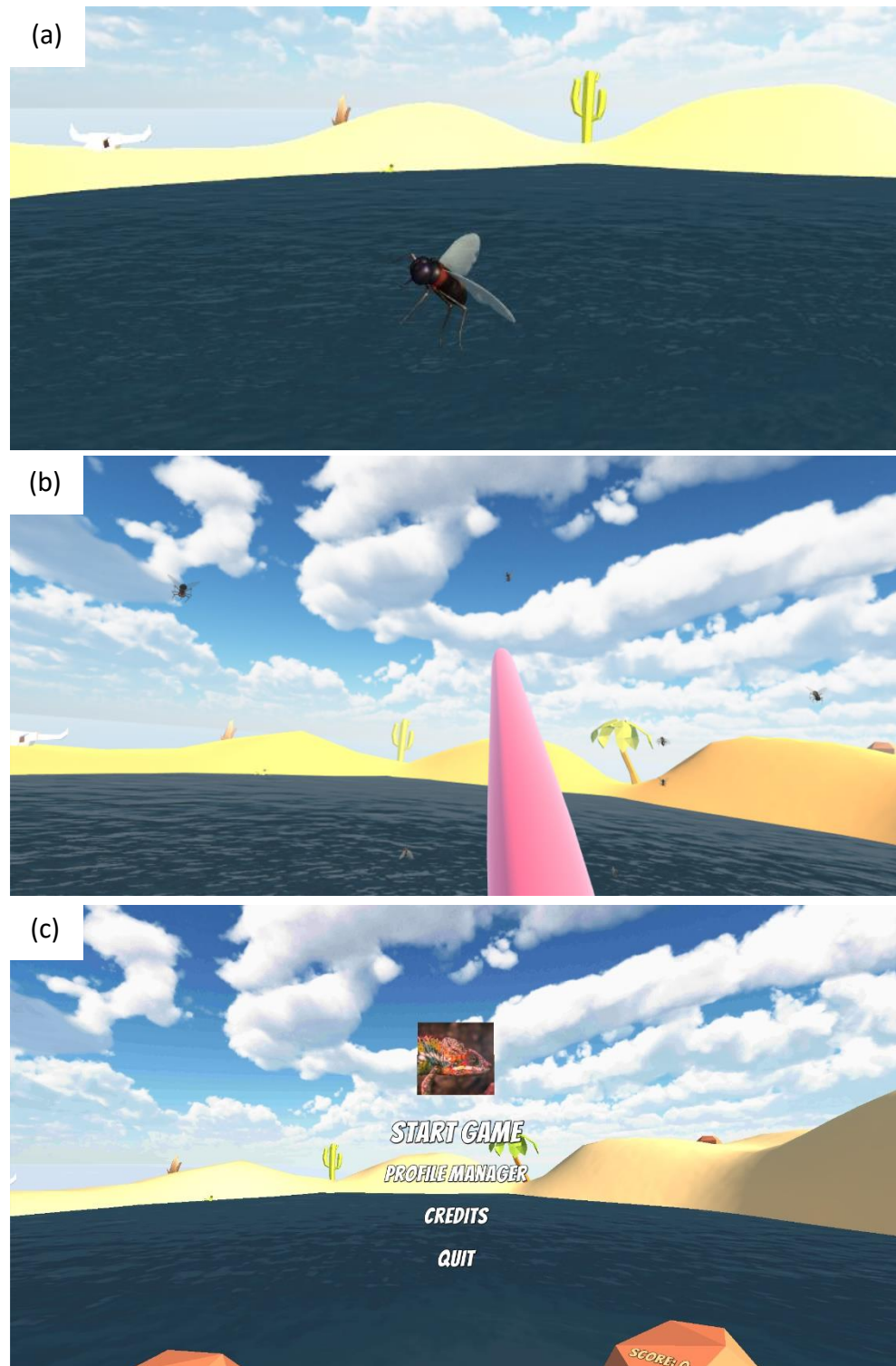
Fig. 4.11 (a) Close up of the fly prey items from the FlyCatcher game (b) In game screenshot of FlyCatcher, note the surrounding flies and the 'tongue' that is projected when the participant presses the 'fire' button (c) In game screenshot of main menu featuring profile picture.

Using these flight characteristics, I generated digital genotypes which consisted of probability mass functions (PMF) for the aforementioned three parameters. In order to provide a large range of complexities of the movement paths observed by human participants, 10000 genotypes were generated. Each genotype contained 5000 PMF's that were normalised and summed into one in order to provide a wide variety of probabilities for movement paths (see Fig.4.5). Furthermore, for each genotype, only one paths was drawn (10000 paths in total). To produce the 10 s flight paths from the genotypes, the same method was used as in experiment one (see 4.2.1.1 Simulations; above). When a participant played the game, they took part in one 'series' of ten trials, each trial consisted of between one and ten prey items. Each of the viewed paths was randomly selected from the available 10000 paths. For each series of trials, no repeated viewings of paths took place. All group sizes were viewed in each series (i.e. each of the ten group sizes was viewed once per series). The order of the trials (in terms of the number of prey items present) was randomised.
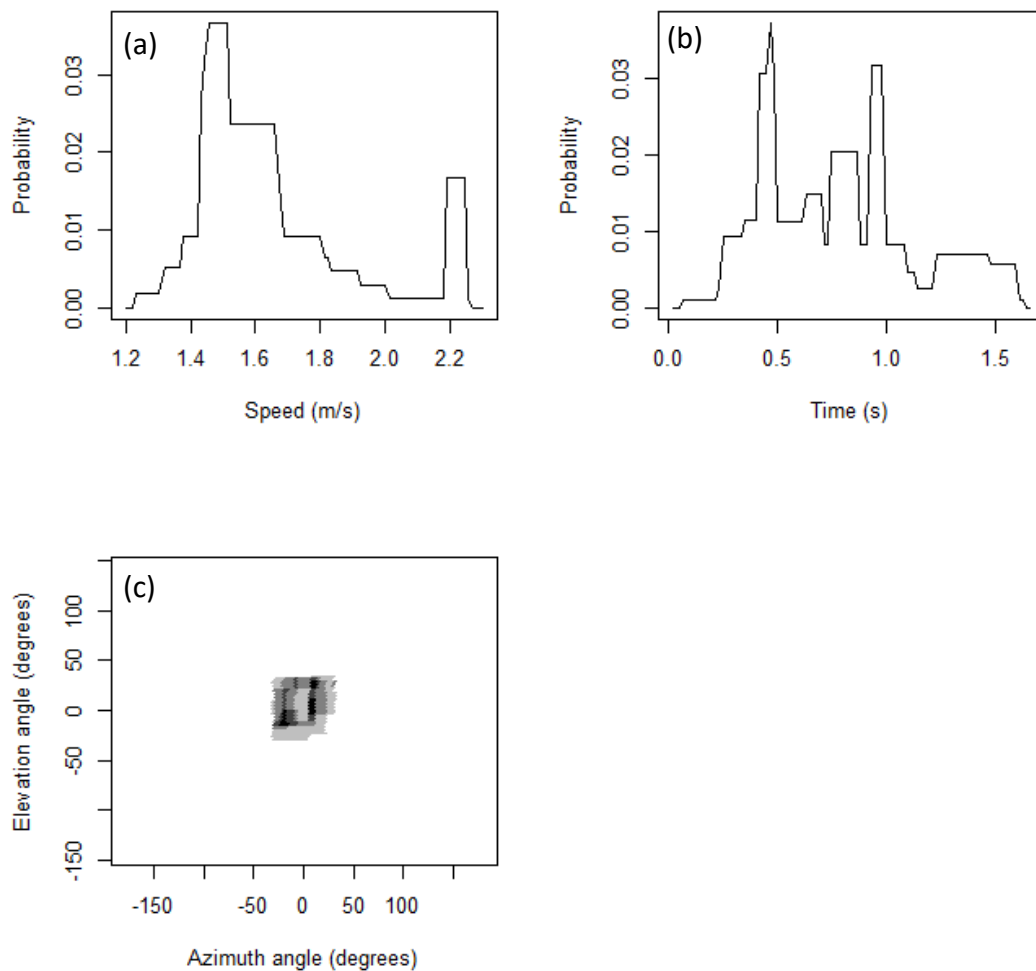
Fig. 4.14 Visualisation of a representative starting genotype: (a) speed, (b) time and (c) turn angle. Note that turn angle is represented in spherical coordinates (azimuth and elevation) with the dark areas representing the probability of those values being drawn from the genotype (darker = higher probability).

4.3.2.2 Experimental protocol

The anonymised nature of this study meant that the number of individual participants that contributed to the data set used in this analysis could not be conclusively determined. However, certain information was recorded in order to approximate the number of individuals that took part in data collection. A unique

identifier for the device which the game was installed upon was accessible to the game and recorded. Furthermore, for each trial series and player profile, an eight-digit alphanumeric code was created and recorded. Using this data, I determined that game data was received from 54 devices. Furthermore, a total of 70 profiles and 84 trial series identifiers were created from which I have inferred that up to 70 individuals submitted game data. Furthermore, several individuals played the game multiple times (hence the larger number of trial series identifiers). Before downloading and installing the game, participants were directed to screen detailing the data that would be shared, to which they had to agree to. Upon starting the game, the main menu appeared (see Fig.4.4) and the participant could either quit, create a new profile, change their profile, or begin a series of trials. Trials would not commence unless a profile was created (if none existed) and selected to represent the participant. Furthermore, when a new profile was created, the agreement to share data was displayed again, which the participants had to agree to in order to begin a series of 10 trials. An instructional screen was presented in advance of each series of trials that briefed the participant to ensure they understood their role in the data collection. Participants saw 10 trials in total consisting of between one and 10 individuals (one trial for each value, so all group sizes were seen by all participants), the order of which was randomised. Each trial presented the participant with a number of prey items that were positioned and orientated within the flight area according to the starting points of the flight paths (text files) that had been generated from the genotype. After a three second visual countdown indicator, the prey items would begin moving according to their flight paths. Participants would then attempt to capture as many individuals as possible within the 10 s time limit. A successful

capture removed the prey item from the trial. If all individuals were captured before the time limit, the current trial ended and the next trial was initiated, and the countdown began. Once all ten trials in a series had been completed, a scoreboard was displayed to participants detailing local records. The main menu then appeared (see Fig.4.4) and the participant could either quit, create a new profile, change their profile, or begin another series of trials if they desired.

4.3.2.3 Data collection

Relevant data was recorded for each capture attempt (i.e. button press) made by participants. Information included the number of flies present (i.e. group size), the path identity of the present flies, the success of the attempt (i.e. failure or capture), the path identity of the caught fly (if applicable) and the device, profile and series identifiers. From this data, the mean path entropy of the flies present in each trial (hereafter referred to as 'mean trial complexity') was recorded, as well as the capture rate (successful attempts divided by total attempts multiplied by 100) for each trial.

4.3.2.4 Statistical analysis

Using the lmer function as above, I tested whether the mean trial complexity value for each trial and group size predicted prey capture rates. I included participant's capture rate as the dependent variable. The number of individuals present in each trial and the mean trial complexity were used as predictors and an interaction was fitted between these two terms. I included trial order as a covariate in order to control for possible learning or fatigue effects over consecutive trials. I also included each participant's anonymous identifiers (device, series and profile identities) as

covariates to control for varying aptitudes for object capturing between participants. Significance was determined by comparing the full model to a reduced model lacking the term of interest using a likelihood ratio test (Crawley, 2005). Finally, I tested whether less complex movement paths were targeted preferentially to more complex movement paths. Full model outputs for all analyses are included in Appendix A.

4.4 Results

4.4.1 Experiment 1 (local data collection)

Contrary to my prediction, there was no interaction between genotype complexity and the number of individuals in predicting targeting distance (χ_4^2 = 6.36, *p* = 0.17). The interaction was therefore removed for the minimum adequate model. I found that the number of prey items present in each trial significantly predicted participant performance (i.e. having a greater mean distance from the targeted prey's centre) (χ_2^2 = 228.21, *p* < 0.001). Specifically, I found that trials displaying five and ten prey items resulted in significantly in poorer targeting accuracy than trials displaying one prey item, though there was no significant difference between five and ten prey items with respect to targeting accuracy (see Fig.4.6a). Furthermore, and also contrary to my predictions, genotype complexity did not predict participant performance (χ_2^2 = 0.19, *p* = 0.91).
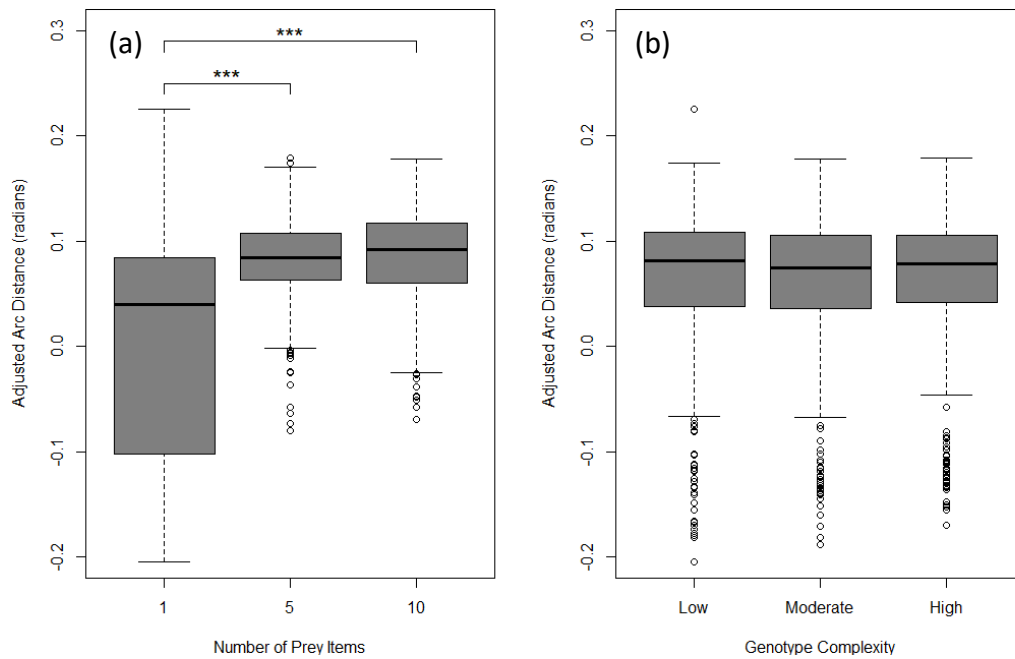
Fig. 4.17 (a) Boxplot displaying the mean targeting distance of participants in each trial against the number of prey items present in each trial. (b) Boxplot displaying the mean targeting distance of participants in each trial against the genotype complexity displayed by prey items in each trial. Asterisks denote significant differences ($p < 0.001$).

4.4.2 Experiment 2 (citizen science)

Contrary to my prediction, there was no interaction between mean trial complexity and group size in predicting capture rates ($\chi_1^2 = 2.29$, $p = 0.12$). The interaction was therefore removed for the minimum adequate model. I found that the group size in each trial significantly predicted capture rates ($\chi_1^2 = 96.53$, $p < 0.001$), with increasing group size corresponding to reduced capture rates (see Fig.4.7). Furthermore, and also contrary to my predictions, mean trial complexity did not predict capture rates ($\chi_1^2 = 0.61$, $p = 0.43$). Finally, the path complexity of early captures was not significantly different to that of the mean trial entropy of remaining paths in trials (where applicable, see Fig.4.8, 4.9) ($t[219.29]=1.23$, $p = 0.22$).
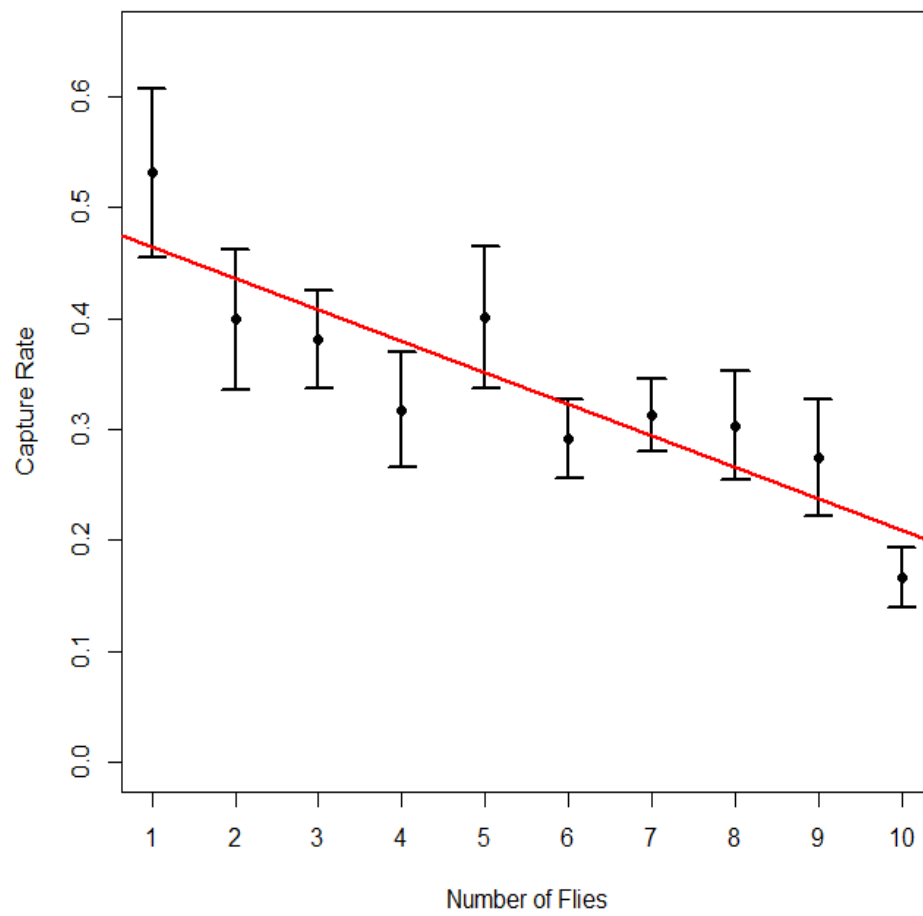
Fig. 4.19 Plot displaying the mean capture rate (± SE) against the number of flies present. Red line represents an lmer model fit.
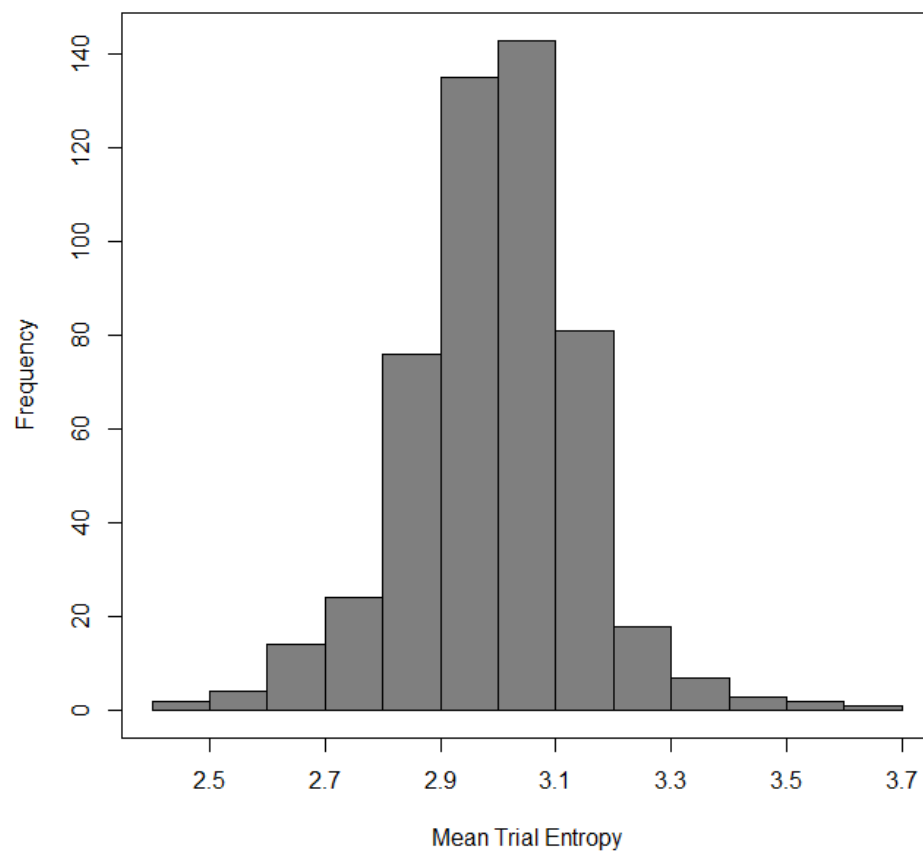
Fig. 4.22 Frequency histogram of mean trial entropy values from collected data.
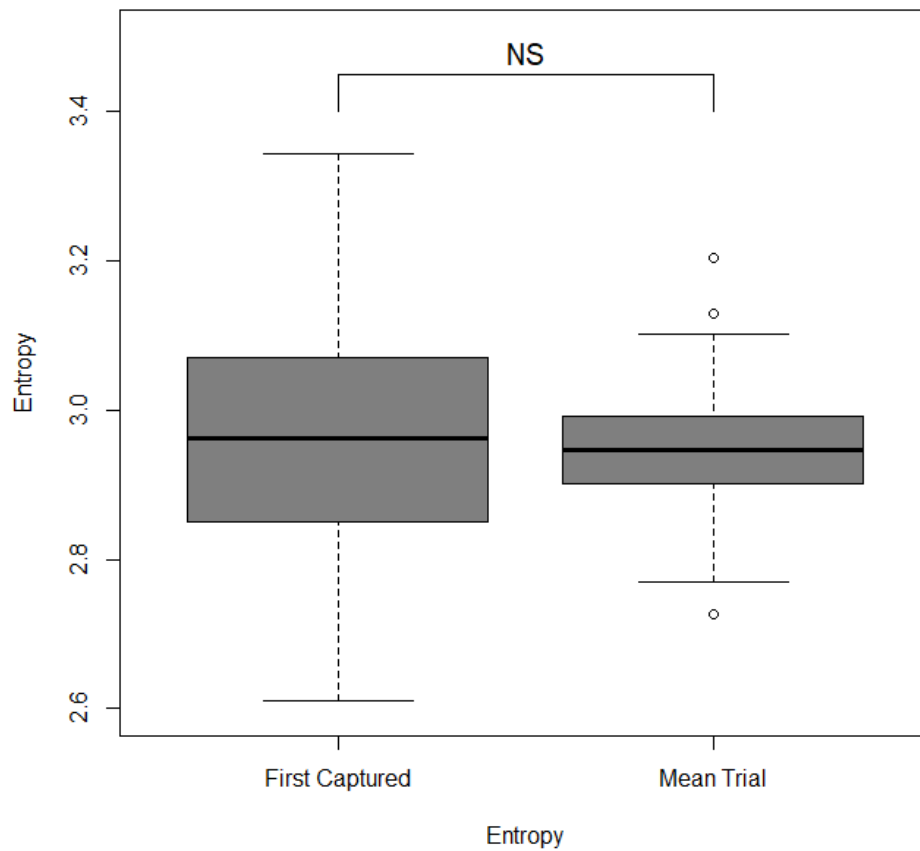
Fig. 4.9 Boxplot showing the entropy values of the first captured individual from each trial in comparison to the mean trial entropy values of remaining individuals from each trial.

4.5   Discussion

Experiment one (local data collection) of this study showed evidence of a confusion effect with increasing numbers of prey items resulting in reduced targeting accuracy when five or ten individuals were present in comparison to when a single individual was present. There was however no significant difference in targeting accuracy between five and ten individuals. Experiment two (citizen science) however, demonstrated a linear decrease in capture rate as the group size presented to human participants increased. Contrary to my predictions however, neither part of the study showed an interaction between prey movement complexity and group size.

Furthermore, and contrary to earlier studies, increasing movement path complexity did not predict poorer targeting or capture rates in either study. Finally, no significant difference was seen between the movement path complexity of the first individuals captured in comparison to the mean entropy of remaining prey items in each trial. The results of both parts of this study are in support of an increase in targeting difficulty or prey capture difficulty with increasing group size as has been demonstrated in a wide variety of other studies (e.g. Hogan et al., 2017; Jeschke & Tollrian, 2007; Jones et al., 2011; Krakauer, 1995). However, my main prediction that increasing protean movement complexity and group size would interact to result in a greater increase in targeting difficulty, was not supported here.

The lack of interaction between complexity and group size in this study aligns my results more closely with those of Jones et al. (2011) and contradicts the findings of Scott-Samuel et al. (2015). Both of these studies consisted of digital animals with human participants as predators. The method of generating movement patterns in these studies differed markedly in comparison to this study. Jones, Jackson, & Ruxton (2011) found that the advantages of protean versus more predictable movements were independent of group size, and therefore protean behaviour did not enhance the confusion effect as they had initially predicted. In contrast to Jones et al.'s (2011) result, Scott-Samuel et al. (2015) reported a confusion effect at higher path unpredictability values that significantly interacted with prey density to predict poorer targeting for human participants. There are a number of potential reasons why the hypothesis is not supported in this study and that of Jones et al. (2011). Indeed, Scott-Samuel et al. (2015) highlighted the divergent results from those of Jones et al. (2011) and offered the differences in stimulus presentation as a potential

explanation. These differences were noted in the introduction. Additionally, another notable methodological difference between the Scott-Samuel et al. (2015) study and that of this study and Jones et al.'s (2011) was target occlusion. In the Scott-Samuel et al. (2015) study, targets always appeared unoccluded to the observer. Specifically, if other prey items (i.e. not the designated target) overlapped on the screen, one appeared to pass in front of the other from the perspective of the observer. The target object however, always passed 'on top' of the object from the perspective of the observer and was therefore always visible. In both Jones et al.'s (2011) study and this study, the targets could occlude one another, which is certainly a real benefit to prey items living in larger groups (Hamilton, 1971) and perhaps goes some way to explain the similarities in findings between this study and that of Jones et al. (2011).

My findings are in support of the conclusion drawn by Ruxton et al. (2007) who found that the confusion effect can occur in uncoordinated movements of prey items. Increasing complexity has been demonstrated to reduce the chances of a prey item being targeted (Herbert-Read et al., 2017; Richardson et al., 2018) but that finding was not replicated here, with increasing movement path complexity having no significant effect on targeting accuracy or capture rates. As the complexity differed significantly between the chosen categories for experiment one (see Fig.4.1) and the mean complexity values displayed in experiment two were also shown to demonstrate a wide range (see Fig.4.8), I was surprised to not observe a similar relationship between participant performance and complexity in the studies detailed here. As the most conspicuous difference between the studies featured in this chapter are the multiple prey items present, I considered that this difference is primarily due to prey item selection by human participants. When predators

encounter groups of prey, they must select a prey individual from the group to target for attack, pursue that prey, and may potentially change the prey item they have chosen to target (Krause & Ruxton, 2002). Furthermore, predators often choose vulnerable prey items that are least able to evade them (Cresswell & Quinn, 2004; Mueller, 1974; Rudebeck, 1950). Multiple prey items allowed predators to switch the prey item they were targeting at will. While individual trials in experiment one (local data collection) consisted of flight paths drawn from the same genotype (and would therefore be similar in behavioural expression), the presence of multiple individuals increased the likelihood that a single prey item would be simpler to target than its group mates (or display a phase of movement that was simpler than it group mates to target). In experiment two, as the paths were drawn from independent genotypes, I therefore expected to see simpler movement paths being more frequently captured first, however this was not the case and no significant difference was seen between the movement path complexity of the first individuals captured in comparison to the mean entropy of remaining prey items. These results lead me to conclude that while the individuals within a grouping benefit from the confusion effect, the advantages conferred by individual protean movements in a group are attenuated. Additionally, the gamification of experiment two resulted in captured prey items being removed from the scene, thereby allowing predators to 'thin the herd' and consequently reduce the confusion effect and facilitating easier capture of additional prey items. Prey selection is of course irrelevant in trials with one individual, but the wider spread of targeting accuracy seen in trials consisting of a single individual in experiment one (see Fig. 4.6a) could indicate that target switching occurred when more prey items were available. It is worth noting however, that quantifying target switching was not

considered during this experimental design and as such using the data available from this study to quantify target switching would be somewhat ambiguous. To elaborate, high prey switching (determined by calculating the nearest prey object to the targets gaze, and how often this changed) could indicate inaccurate or poor targeting of individuals (i.e. the participant regularly drifts from a chosen prey item to the point where gaze is closer to another prey item). It could however be taken to mean that a participant was regularly and accurately switching to easier targets as they presented themselves (a combination of these two possibilities is also plausible on an intra and inter-trial basis). It is for this reason that I did not pursue analyses using target switching in this study.

While I have shown here that the confusion effect can occur in uncoordinated movement, coordinated groups can seemingly amplify the overall impact of the confusion effect with respect to predator targeting or capture of prey items. For example, Ioannou et al. (2012) studied bluegill sunfish (*Lepomis macrochirus*) predating upon mobile virtual prey. In this study, Ioannou et al. (2012) demonstrated that when prey items displayed coordinated movements (i.e. prey items moving in aligned directions and with stable inter-individual separations), the resultant confusion effect was significantly stronger in comparison to that induced by uncoordinated movements with comparable movement characteristics. Indeed, Herbert-Read et al. (2013) showed that the individuality of movement patterns in mosquitofish (*Gambusia holbrooki*) in asocial contexts was reduced when introduced to groups of conspecifics (the larger the group, the greater the attenuation of individuality). Furthermore, the variation in the individual's preferred speeds were reduced, presumably resulting in reduced movement complexity. It is plausible that

the energetic expenditure of engaging in more complex unpredictable movements is assessed as a poor investment relative to that offered by associating and conforming with a group and gaining the benefits of the confusion effect resultant from a coordinated shoal or flock. Furthermore, in the same way that conspicuous colouration of an individual (relative to other group members) can facilitate preferential targeting via the 'oddity effect' (Landeau & Terborgh, 1986), conspicuous movement (e.g. more complex protean movement) may engender the same effect. This hypothesis is explored in chapter five.

In summary, this study supports the presence of a confusion effect as a predictor of poorer targeting accuracy for human predators. Existing literature studying the interaction between the confusion effect and movement path complexity is equivocal. Here, however, I have found no evidence of an interaction between the two. This is comparable to the findings of Jones et al., (2011). This result shows no evidence of an interaction between movement path complexity and group size when considering small groupings of uncoordinated movements representative of real animal movements.

5. Behavioural Oddity and Anti-Predator Movement

5.1 Chapter Abstract

In animal groups, individuals that are phenotypically distinct from the rest of the group can be preferentially targeted by predators in a process known as the 'oddity effect'. Oddity has generally been assessed with regard to morphological features such as size and colour, but differences in movement behaviour may also represent a potential source of oddity. Using human 'predators' participating in 3D virtual reality simulations in which they were tasked with targeting erratically moving (i.e. 'protean') swarming prey, we show that virtual prey displaying 'odd' movement patterns are targeted preferentially, and with greater accuracy, than other members of their group. Our results indicate that behaviourally odd movement paths displayed by an individual within a group significantly increase its risk of predation. This finding provides further insight into the nature of anti-predator movement with respect to the selection pressures that exist among group living organisms.

5.2 Introduction

The formation of groups shown by many animal species is a commonly observed and well-studied phenomena. Group membership most often incurs costs for individuals, with the primary disadvantages being an increase in resource competition and a greater likelihood of conflicts regarding reproduction (Alexander, 1974; Hamilton & May, 1977). Further disadvantages include increased visibility to predators, parasite loading, and disease transmission rates (Neems, Lazarus, & Mclachlan, 1992; Wilson, Knell, Boots, & Koch-Osborne, 2003). However, while these costs are non-trivial,

there are a wide variety of benefits that can arise from group membership that typically result in a net benefit to the individual, hence the ubiquity of animal groups in nature. Such benefits include increased foraging efficiency (Pitcher, Magurran, & Winfield, 1982; Rubenstein, 1978) and higher reproductive success (Ward & Webster, 2016). Furthermore, among the most influential advantages are the variety of anti-predator benefits that are associated with animal groupings. Examples of benefits that can be conferred by group living include the dilution effect, where the chance of capture for any one individual reduces as group size increases (Morgan & Godin, 1985), selfish herding, where individuals adjust their position to put other group members between themselves and predators (Hamilton, 1971), increased group vigilance and alarm calls due to many individuals being more efficient at detecting predators (Davies, Krebs, & West, 2012) and the confusion effect (Landeau & Terborgh, 1986; Penry-Williams et al., 2018).

Whilst being a member of a group can reduce predation risk via the mechanics listed above (Elgar, 1989; Godin, 1986; Miller, 1922; Sridhar, Beauchamp, & Shanker, 2009), an individual may be selectively targeted if it is phenotypically 'odd' with respect to other members of its group, in a phenomenon known as the 'oddity effect' (Aivaz, Manica, Neuhaus, & Ruckstuhl, 2020; Mathis & Chivers, 2003; Penry-Williams et al., 2018; Raveh, Langen, Bakker, Josephs, & Frommen, 2019). In effect, the oddity of an individual prey item (or several prey items) may draw the attention of a predator and thereby overcome the detriment to targeting imposed by group anti-predator benefits (Rodgers, Ward, Askwith, & Morrell, 2011; Ruxton et al., 2007; Tosh et al., 2006; Tosh & Ruxton, 2006). This can result in not only the preferential targeting of the odd individuals, but also greater capture rates overall,

regardless of oddity (Aivaz et al., 2020; Landeau & Terborgh, 1986). Most evidence supporting the oddity effect concerns morphological oddity, particularly in terms of characteristics such as colouration and size. Examples for the former come from Landeau & Terborgh (1986) who used the predatory largemouth bass (*Micropterus salmoides*) and silvery minnow prey (*Hybognathus nuchalis*). They found that the inclusion of one or two 'odd' (blue-dyed) minnows in a school of eight greatly increased the ability of bass to capture both normal and odd prey, with the oddity effect disappearing at school sizes of fifteen or above. Additionally, Rutz (2012) found that goshawks (*Accipiter gentilis*) selectively kill rare colour variants of their principal prey, the feral pigeon (*Columba livia*). Regarding size oddity, Theodorakis (1989) also used the largemouth bass (*Micropterus salmoides*) as a predator and found they favourably attacked odd-sized prey individuals in three different minnow species (*Pimephales notatus*, *P. promelas* and *Campostoma anomalum*). Furthermore, it has been demonstrated that prey animals prefer to associate with colour and size matched conspecifics, particularly under the threat of predation (Blakeslee et al., 2009; Krause & Godin, 2010; McRobert & Bradner, 1998; Wolf, 1985). Interestingly, there is indirect evidence suggesting that oddity effects can also result from conspicuous movement with respect to their grouping. For example, Herbert-Read et al., (2013) quantified the individuality of the locomotory behaviour (i.e. median speeds, variance in speeds and median turning speeds) of female mosquitofish (*Gambusia holbrooki*) when tested on their own and found that individual variance was suppressed when they were part of groupings of conspecifics. The prevention of an oddity effect was cited as an explanation for the finding. In another example, Szulkin, Dawidowicz, & Dodson (2006) found that when groups of *Daphnia pulicaria*

were exposed to olfactory cues of common predators, they responded by increasing the uniformity of their swimming behaviour, the authors suggested that minimising the 'behavioural oddity' among group members served to decrease predation risk (Szulkin et al., 2006).

While there is little direct evidence to support the preferential and more accurate targeting of behaviourally odd individuals, it is well established in human psychology that eye movements are drawn towards conspicuous or odd visual stimuli with greater in what is known as the 'pop-out' effect (Adler & Orprecio, 2006; Dannemiller, 2002). Early studies identified this phenomenon using a series of homogenous distractors with one or several uniquely coloured or patterned individuals amongst them (Treisman, 1985; Wolfe, 1994), in scenarios analogous to morphologically odd prey. However, later work quantified the pop-out effect in contexts more applicable to animal motion, for example, Rosenholtz (1999) developed a model for predicting the ease of identifying individuals moving with odd speeds, based upon a quantitative measure of target saliency. The term target saliency is primarily used in psychology literature and refers to the quality (or qualities) of a stimulus that contribute to its detectability to an observer (VandenBos, 2007). Rosenholtz (1999) concluded that identifying an odd target would be easier the more the target motion deviates from the general pattern of speeds in the scene (Rosenholtz, 1999). However, psychological studies into the pop-out phenomena are typically focussed on its effect on human search behaviour and (as it has been demonstrated that oddity of speed is more discriminable than oddity in other aspects of movement [e.g. direction]) rarely incorporate multiple aspects of movement simultaneously (Borji, Sihite, & Itti, 2013; Ivry & Cohen, 1992; Wolfe, 1994). These

psychological studies focussed on simpler movement patterns and were not designed to investigate the oddity effect in the context of animal motion. Furthermore, the movements displayed and were not aimed to mimic animal movements. Despite substantial evidence demonstrating the salience of conspicuous movements, to our knowledge, no study has directly examined the oddity effect with respect to movement patterns representative of animal motion.

As the principle of the salience of an oddly moving object among a group (using simple movements that only vary in one aspect) has been established, I am therefore interested here in the more complicated patterns that represent a moving animal. Individual animals within groups may reduce their chances of predation via unpredictable movements (Jones et al., 2011). The complexity (Shannon entropy) of movements has previously been suggested as a predictor of anti-predator movement effectiveness (Herbert-Read et al., 2017). Chapter two's findings were in support of this theory, but also found there were many different ways to move unpredictably which are similarly effective at evading predators (Richardson et al., 2018). If an individual displays a *novel* unpredictable movement pattern with respect to other individuals in its group (i.e. an odd movement pattern), can it 'pop-out' and appear visually conspicuous or odd to potential predators? In chapter two, I used a 3D virtual reality (VR) simulation with human 'predators' targeting 'prey' items to test the effect of oddity of movement on a predator's ability to target moving prey items (Richardson et al., 2018). The use of virtual prey in animal behavioural research is becoming more common (Bond & Kamil, 2002, 2006; Duffield & Ioannou, 2017; Ioannou et al., 2012; Jones et al., 2011; Richardson et al., 2018) and has recently been used in the study of the oddity effect, demonstrating the validity of this approach

(Dobbinson et al., 2020). Psychology literature has established that conspicuous targets can result in preferential and more accurate targeting than less conspicuous targets (Findlay, 1997; Krakauer, 1995; McSorley & Findlay, 2003). In this chapter I examined these effects in the context of more complicated patterns representing animal movement paths. I hypothesised that odd movement behaviour can induce a behavioural oddity effect that results in the odd individual being preferentially, and more accurately, targeted compared to all other 'conformist' (i.e. morphologically identical individuals that move with rules identical to one another, but differing from the odd individual) members of the odd individuals group. Additionally, I predicted that the targeted odd individuals would show greater movement path complexity (an indicator of protean movement efficacy) than targeted conformist individuals.

5.3   Materials & Methods

5.3.1   Simulations

Similar to chapter two (Richardson et al., 2018), all simulations were created in the Unity3D game engine running on a Microsoft Windows PC, and built to run on a Samsung Galaxy S7 smartphone using the Samsung Gear VR system.

Simulations consisted of ten black spheres (the 'prey') presented against a homogenous white background to maximise contrast. The prey moved in a 3D virtual space centred on a point 30 m directly in front of the participant. The prey items moved within a spherical area with a diameter of 20 m. Within the simulation, participants were free to look around the virtual environment. A small, red circle (the reticle) was superimposed onto the centre of the participants' field of view and provided a point of reference for the participant to facilitate targeting, allowing them

to interact with moving prey item in real time. The dimensions of this 'flight area' facilitated the simulation of a grouping of animals (i.e. swarming insects such as midges) and ensured prey movement stayed within a comfortable range of motion for all participants with respect to their head movements. This had two primary benefits. First, it kept all individuals within the participant's field of view, so the odd individual was always visible to the participant in experimental trials. Secondly, it allowed us to isolate protean movement efficacy in terms of head movements alone, rather than a combination of head movements and the noise introduced by the reorientation of participants' bodies to target objects that have moved outside of their comfortable range of motion.

Prey movement used similar principles to the prey items in chapter two, namely a series of steps during each of which it travelled in a straight line in 3D space before turning and moving off on a different trajectory. Movement of prey in the simulation was determined by three parameters: the speed at which the prey moves within the virtual environment in metres per second (hereafter referred to as 'speed'), the angle in degrees turned within a cone centred on the prey's direction of travel (hereafter termed 'angle') and the time in seconds until the next turn (hereafter termed 'time').

The next step was to decide the parameter space of the prey items movement characteristics. In chapter two, I found that higher speeds were the most influential component with respect to increasing targeting difficulty. In this study, as I are mainly concerned with demonstrating a behavioural oddity effect, I wanted movement paths that could vary in appearance greatly, but not have the extremes of flight

movement be too challenging to target for participants. I therefore chose a maximum speed value of 15 ms^{-1} as I found (through pilot experiments) that this represented a suitable compromise between these two objectives. Our speed range was therefore between 0 ms^{-1} and 15 ms^{-1}. The maximum turn angle value was also decided with the same mindset as the maximum speed value. The angle search space constrained the widest possible turn to 45° (0.25 π radians), thereby putting the range of angle values between 0 and 0.25 π radians. Finally, for the time characteristic, the maximum value was decided based on the amount of time it would take a prey item moving at maximum speed to get from the swarm centre to the edge of the flight area. The lower value was based on the frame rate of the simulation (50 Hz). This put the range of time values from 0.02 s to 0.66 s.

Using these flight characteristics, I generated digital 'genotypes' which consisted of probability mass functions (PMF) for the aforementioned three parameters, using a similar method to that of chapter four. Discrete uniform distributions between two randomly generated values within each parameter search space were generated. Through pilot data I found that two sets of these discrete distributions (summed and normalised to create one PMF [genotype]; see Fig.5.1) frequently resulted in clear and consistent variation in the appearance of the flight paths between different genotypes. Additionally, I found that even when genotypes contained extreme values for their flight characteristics, it was challenging, but not impossible to maintain targeting.

In order to produce behaviourally odd individuals, I generated genotype pairs that were similar in the complexity of their probability distributions but had a large

mathematical difference between the shapes of their distributions. To this end, I

used a type of f-divergence known as the Hellinger distance (*H*: see 5.1, where *p* =

genotype A probability mass function, [$p_1 … p_n$] and *q* = genotype B probability mass

function, [$q_1 … q_n$], also see Fig.5.1).

$$H = \sqrt{\left(1 - \sum_{i=1}^{n} \sqrt{p_i * q_i} \right)} \qquad\qquad 5.1$$

This value compares two distributions and returns a number between zero

and one, with zero indicating an identical distribution and one indicating a

completely different distribution with no overlap (i.e. no shared values between the

distributions). To create our behaviourally odd individuals, I created genotype pairs

with Hellinger distances of 0.95 and used these to generate flight paths. Unique

genotype pairs and flight paths were generated for each participant. Once all

genotypes corresponding to movement characteristics had been created, flight paths

could then be produced.

To produce flight paths from a genotype, firstly, a starting position was

randomly generated within the flight area. Secondly, the initial speed, angle and time

were randomly selected from the genotype. Then, the trajectory of a prey item

moving according those values was recorded in cartesian coordinates and added to

a text file. When the time value was reached (i.e. the number of frames

corresponding to the initial time value in seconds), new values of speed, turn angle

and time until turn were drawn from the genotype. This process continued until

either

1. The trajectory passed out of the flight area, whereupon it would turn back toward the swarm centre as rapidly as its genotype movement rules allowed.

2. Ten seconds of trajectory data had been generated, whereupon the text file containing the path coordinates was saved.
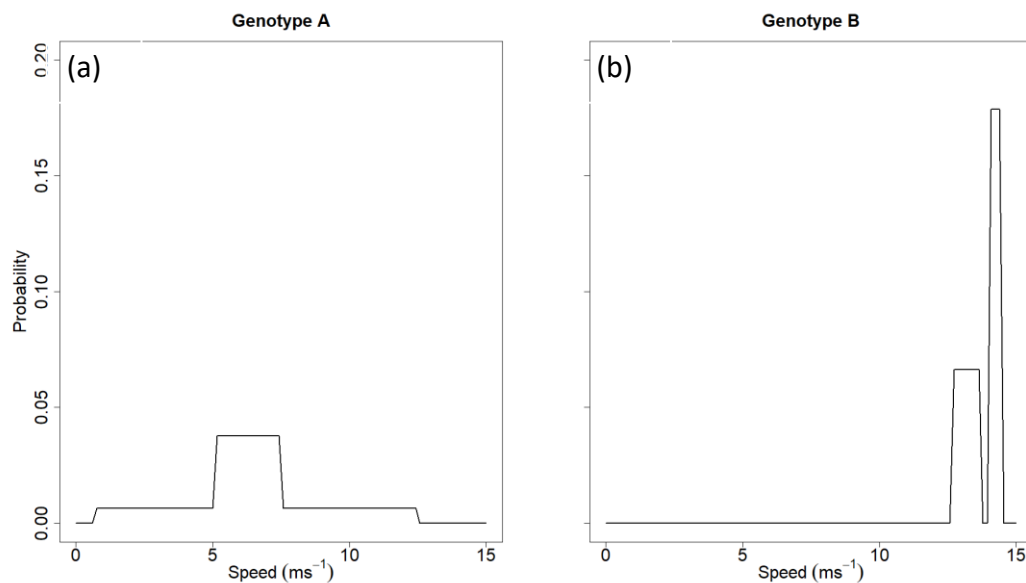
Fig. 5.2 Example distribution for a genotype pair, in this case, speed. Frequency values sum to one. Note the flatter, combined distribution in panel a (genotype A), compared to the separate, narrower distribution in panel b (genotype B).

5.3.2 Experimental protocol

A total of n = 40 participants took part in this study (25 females, 15 males; mean age = 20.7 [range, 19 − 45]), all of whom were staff or students at the University of Lincoln. Before providing consent to take part in the study, participants were given written information on the general aims of the study (although not the specific hypotheses being tested), what they would be asked to do, and the approximate time required to complete the study. Their age and gender were reported (but not linked

to their experimental data). This project was approved by the College of Science ethics committee at the University of Lincoln (reference CoSREC265). After consent was given, a detailed verbal briefing was given to each participant to ensure they understood their role in the data collection.

Participants saw 30 trials in total (20 experimental, 10 control [see table 5.1.]). For each genotype pair, participants saw three trials in total (two experimental trials and one control trial). One experimental trial consisted of nine prey items from one genotype of the pair and a single odd prey item from its corresponding paired genotype. The other experiment trial was a counterbalanced version of the first in order to ensure that both genotypes in each pair were represented as odd and conformist individuals. Participants also saw one control trial consisting of five individuals of each genotype (and therefore no individuals were odd). Participants put on the headset and familiarised themselves with the VR environment. Once the participant indicated they were ready, the experimenter began the simulation, starting with the three training trials. The training trials consisted of ten individuals that would begin moving (after a three second visual countdown indicator) according to 'training genotypes'. There were no odd individuals present in these trials. The movement characteristics of each training genotype got progressively more extreme (i.e. higher speed and angle values, with lower time values) with each trial in order for the participant to familiarise themselves with the types of movement behaviours they would be observing. Once the training trials were completed, and participants indicated they were comfortable with targeting prey items within VR, the experimental testing trials began. Training trials were repeated if requested by participants. Each trial presented the participant with ten prey items that were

positioned and orientated within the flight area according to the starting points of the flight paths (text files) that had been generated from their genotypes. After a three second visual countdown indicator, the prey items would begin moving according to their flight paths. For all trials, each participant was instructed that they were to choose any single prey item and target it as accurately as they could. In this case, accurate targeting referred to maintaining the targeting reticle on the centre of the chosen prey item (or as close to the centre of the chosen prey item as they were able) via their head movements. Crucially however, participants were instructed that they were free to change the object they were targeting at any time, for any reason. The only condition was that they were always attempting to target a prey item as accurately as possible throughout each experimental trial. The order of the experimental trials was randomised for each participant.

Table 5.1 Breakdown of experimental treatments. Each participant saw movement paths from ten unique genotype pairs in total, with three conditions for each. Each trial consisted of ten prey items. For control trials, participants saw five individuals from each genotype, and therefore no individuals were 'odd'.

Genotype Pair Treatment	Number of Individuals (Genotype A)	Number of Individuals (Genotype B)
Experimental 1	1	9
Experimental 2	9	1
Control	5	5

5.3.3   Data collection

Telemetry data of the participant's head orientation (a 3D vector passing through a point between the participant's eyes and towards the reticle) were collected every 0.02 s throughout each trial (this method of telemetry recording was used in chapter two [see Richardson et al., 2018]).

Due to the multiple objects present in view in each trial, I quantified object targeting using the same method as chapter three (i.e. calculating arc distance between participant gaze and prey items). The prey item with the smallest arc distance between the participants gaze and itself was considered to be the item being targeted for that frame and the value of this metric indicated the accuracy with which that prey item was being targeted (i.e. a smaller arc distance indicated more accurate targeting than a larger arc distance). I also compared the proportion of time prey items were targeted depending on the individual type (i.e. odd, conformist or control). For experimental trials, I compared the proportion of time the odd type individual was the targeted object compared to a randomly selected conformist type individual. In control trials, I randomly selected a single individual (i.e. a control type individual) in order to compare these values to the experimental trial proportions. Significant differences between targeting proportions by individual type would indicate a target preference.

The general consensus within psychology literature suggests that in visual search tasks with adult humans, stimuli displaying unique perceptual feature(s) 'pop out' from dissimilar distractors and usually detected within 500 milliseconds by the observer (Adler & Orprecio, 2006). Here, participants were not instructed to search for an odd object and could switch at will. A trial time period of ten seconds was chosen to allow for any behavioural oddity based pop-out phenomenon to occur, and give substantial targeting data to evidence that odd objects were targeted preferentially and more accurately than conformist objects.

5.3.4   Statistical analysis

All analyses were conducted using general linear mixed-effects models (glmm) in R version 3.5.2, using the lmer function in the lme4 package (Bates et al., 2015). The validity of the model assumptions was confirmed by visually assessing the normality of the model residuals. Firstly, I tested whether oddity predicted how accurately participants targeted prey items. I included participant's targeting accuracy in radians (log transformed) as the dependent variable. The condition of the individual (i.e. odd, conformist or control) was used as a predictor. I included trial order as a covariate in order to control for possible learning or fatigue effects over consecutive trials. I also included each participant's anonymous identifier as a covariate to control for varying aptitudes for object targeting between participants. Finally, I included the genotype identifier as a random effect to control for repeated viewings of each genotype (i.e. each participant saw three trials with the same genotype pairs). Significance was determined by comparing the full model to a reduced model lacking the term of interest using a likelihood ratio test (Crawley, 2005).

Secondly, I tested whether oddity predicted participants' targeting preference. This preference was quantified via the proportion of time participants targeted a prey item. To extract this figure, I calculated the number of frames that relevant individuals (i.e. odd, randomly selected conformist, or randomly selected control) were targeted in each trial. I then divided that value by the total number of frames per trial (500). This resulted in a value between zero and one, with higher values representing a greater proportion of time targeting that individual. This value was included as the dependent variable, with the individual type (i.e. odd, conformist

or control) as a categorical predictor. The covariates and random effects were the same as the previous model. Significance was determined using the same method as above. Furthermore, if an individual prey item's type (i.e. odd, conformist or control) had no effect on the proportion of time it was targeted, this value should not differ significantly from chance (i.e. targeted ~10% of the time). To that end, I performed two-tailed one sample t-tests on the proportion of time targeted data for each prey type against a comparison value of 0.1. Statistically significant results ($p < 0.05$) would indicate that the proportion of time targeted for the relevant prey type differed from chance.

Finally, I tested whether the prey items that were targeted in experimental trials differed in their movement path complexity with respect to the prey type (i.e. odd vs conformist individuals). Using the accuracy data from part one of the analysis, I calculated the movement path complexity (entropy) of each individual that was targeted in experimental trials. This value was included as the dependent variable, with the individual type (i.e. odd or conformist) as a categorical predictor. The covariates and random effects were the same as the previous model. Significance was determined using the same method as above. Full model outputs for all analyses are included in Appendix A.

5.4 Results

5.4.1 Targeting accuracy

The identity of the prey item (odd, conformist or control) significantly predicted the accuracy with which participants targeted prey items (χ^2_2 = 4310.31, p < 0.001). Odd individuals were more accurately targeted (i.e. had a smaller mean distance from the prey's centre) than both the conformist individuals accompanying them in the same trial (0.25±0.00, t = 65.72, df = 599800, p < 0.001) and individuals presented in separate control trials (0.19±0.01, t = 25.57, df = 1.418, p < 0.001).
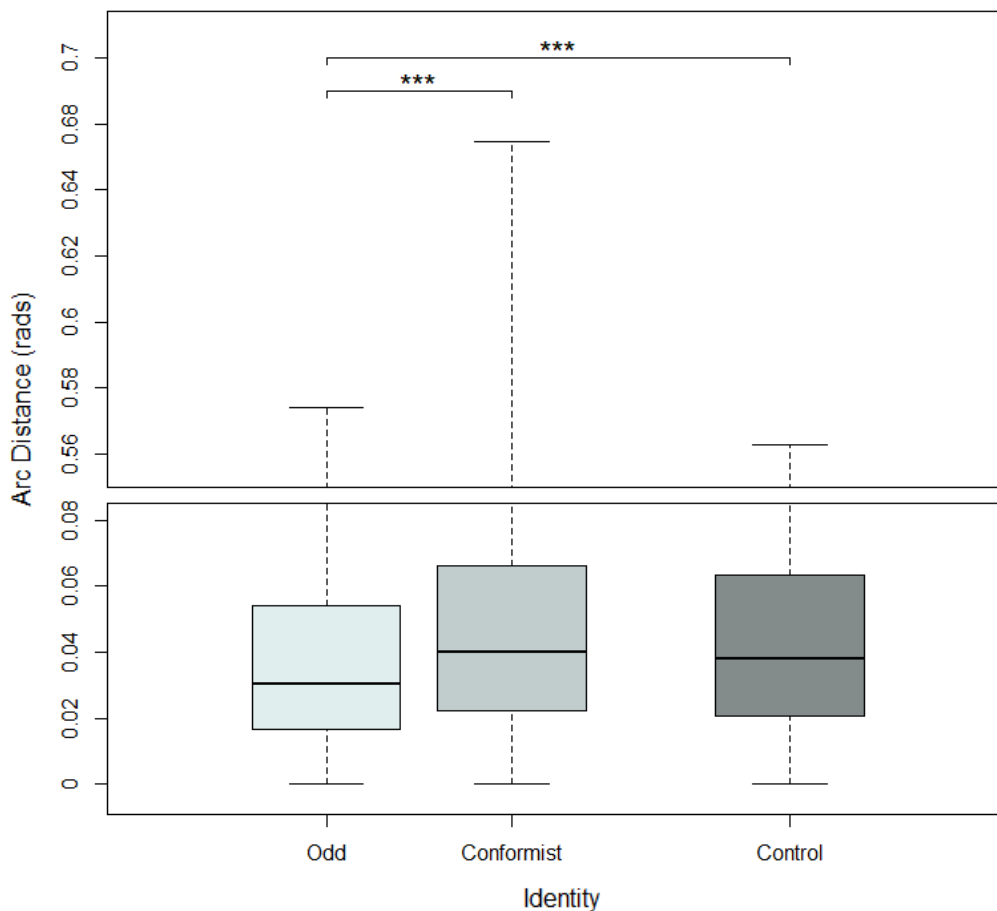
Fig. 5.3 Gapped boxplot showing the targeting accuracy (arc distance from the centre of the prey [radians]) as a function of experimental condition. Asterisks denote significant differences (***, p < 0.001) between conditions.

5.4.2 Proportion of time targeting

Individuals displaying 'odd' movement behaviour were targeted for a significantly greater proportion of time than other (conformist) members of their group (χ^2_2 = 15.39, *p* < 0.001; Fig.5.3). Odd individuals were targeted for higher proportions of time than conformist individuals (3.63±0.01, *t* = 3.12, df = 1995, *p* = 0.001), resulting in an odd individual being 1.33 times more likely to be targeted by a participant than a control individual. There was no significant difference between the proportions of time targeted for conformist and control individuals (-0.01±0.01, t = -.834, df = 1995, *p* = 0.40). Only odd individuals showed a significantly higher proportion of time targeted than chance (*t*[799]=5.24, *p* < 0.001), indicating preferential targeting.
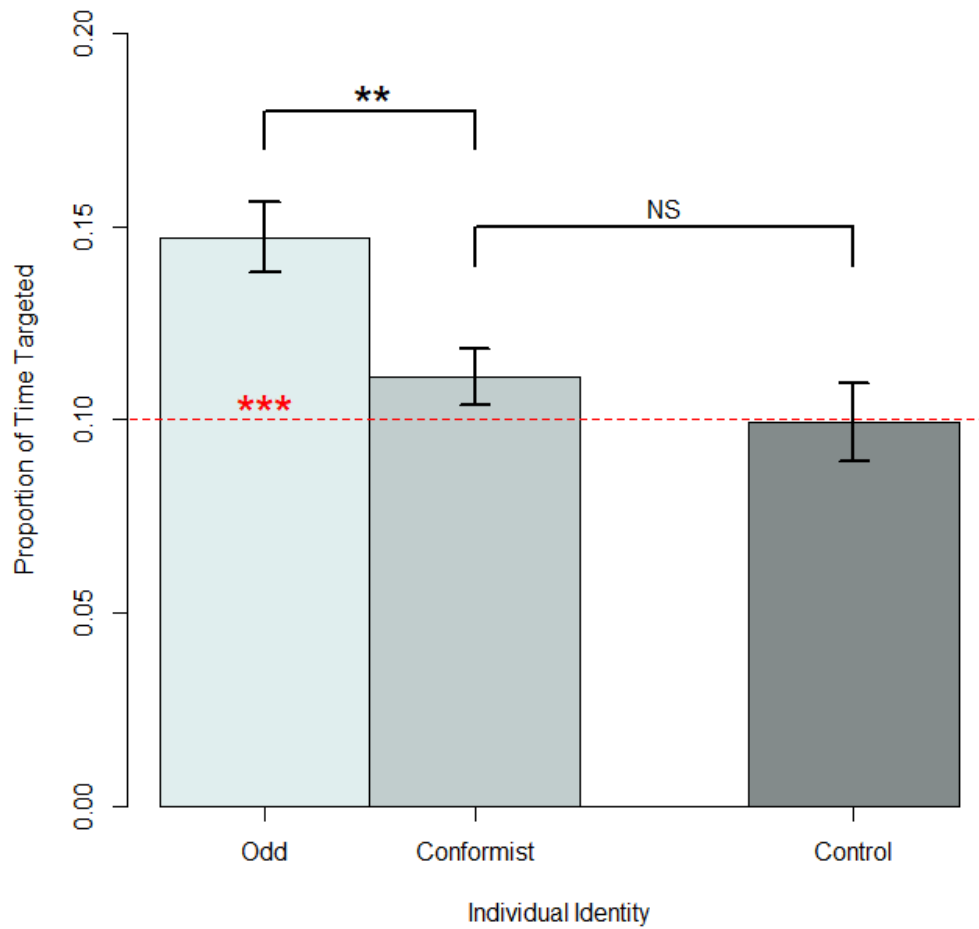
Fig. 5.6 Mean ± SE proportion of time participants targeted objects as a function of condition. The left two columns show the odd individual and a randomly selected conformist individual from each experimental trial. The right column shows a randomly selected individual from each control trial. The black asterisks (**) denote a significant difference ($p = 0.01$) between odd and conformist individuals with respect to the mean proportion of time they were targeted, while 'NS' indicates no significant difference between the randomly selected conformist and control individuals with respect to the mean proportion of time they were targeted. The horizontal dotted line represents where values should sit if they are targeted by chance alone (i.e. targeted 10% of the time). The red asterisks (***) denote a significant difference ($p < 0.001$) from chance for odd individuals

5.4.3   Targeted item complexity and prey type

When comparing the difference in movement path complexities between odd individuals and the 9 conformist individuals that were displayed alongside them in each individual trial, the range of entropic differences was normally distributed, where odd individuals were equally likely to move in more, or less complicated patterns than conformists (see Fig. 5.4).

Experimental Trial Flight Paths
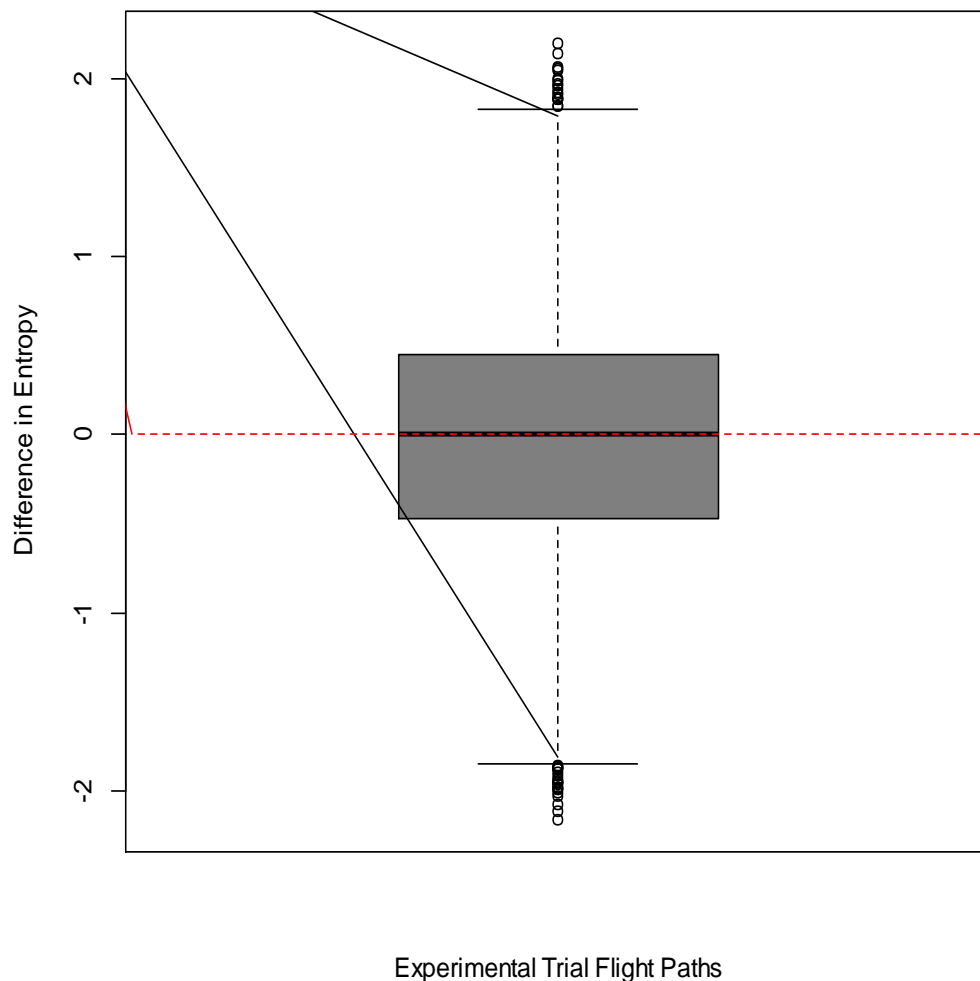
Fig. 5.4 Boxplot showing the spread of differences in entropy values between odd individuals and the conformist individuals that were displayed within each experimental trial. Data above the red line indicates that an odd individual flight path was more complex than a conformist flight path that was displayed in the same trial. Data below the red line indicates that an odd individual flight path was less complex than a conformist flight path that was displayed in the same trial.

The movement path complexity of odd individuals that were targeted by human participants in experimental trials were not significantly different from that of targeted conformist individuals ($\chi^1_2 = 0.45$, *p* = 0.5; Fig.5.5).
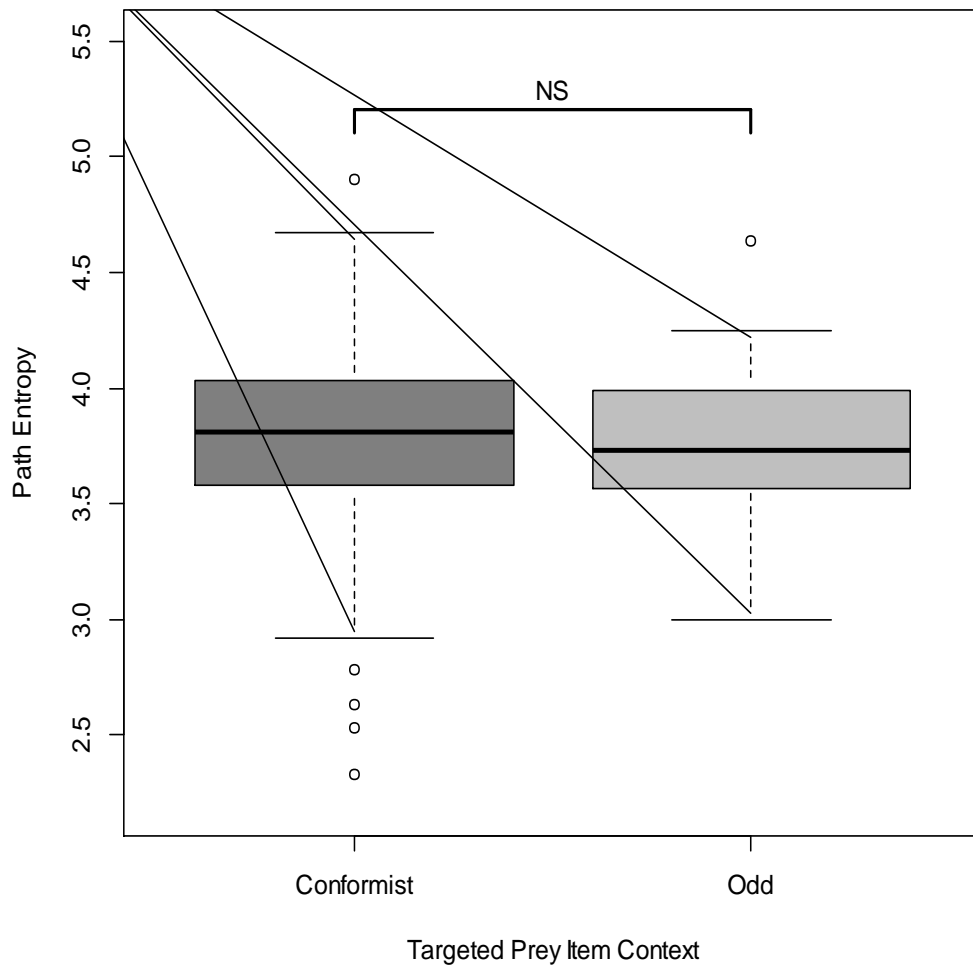
Fig. 5.5 Boxplot showing the flight path entropy values of targeted odd and conformist individuals that were displayed in experimental trials. 'NS' indicates no significant difference between the entropy values of the two categories.

5.5   Discussion

In this study, I have shown that individuals that move differently with respect to the rest of their group are preferentially and more accurately targeted. This supports our hypothesis that animal movements can induce a behavioural oddity effect.

Furthermore, the movement path complexity of targeted individuals showed no significant difference between prey types in experimental trials (i.e. odd vs conformist). This indicates that the behavioural oddity effect was equally likely to occur whether the movement patterns of the odd individual were more or less complex (an indicator of protean movement efficacy) than conformist prey items .

While groupings of animals provide many benefits, including the confusion effect, there are also significant potential costs. These include more intense competition, increased conspicuousness to predators and increased disease and parasite transmission rates (Alexander, 1974; Neems et al., 1992; Wilson et al., 2003). Assessing the cost-benefit relationship of joining a group as accurately as possible would be advantageous and would include considering the oddity effect. The generally accepted explanation for the oddity effect is that the targeting of individuals that appear distinct from an animal grouping is less cognitively demanding for the predator, partially nullifying the confusion effect (Penry-Williams et al., 2018). When given the opportunity to join a group, many animal species appear to consider the characteristics of the group with respect to themselves. Similar characteristics often result in an increased likelihood of joining the group. For example, animals have been shown to prefer groups of similar colouration, activity levels and body size (Blakeslee et al., 2009; McRobert & Bradner, 1998; Pritchard, Lawrence, Butlin, & Krause, 2001; Ranta, Lindström, & Peuhkuri, 1992; Rodgers et al., 2011). By joining groups that are homogenous relative to themselves, animals reduce the likelihood of an oddity effect occurring. So, prey animals can perceive physical and, crucially, behavioural differences within groupings and appear able to use this information to inform their decision on whether to join a group or not. It is unknown whether this

perceptual ability extends to the detection and assessment of compatible movement strategies, but such an ability would be advantageous.

As demonstrated in chapter two, with respect to anti-predator movements, movement path complexity (entropy) is a general indicator of protean movement efficacy (Richardson et al., 2018). In this study, the distributions that represented the movements observed by participants were generated at random (and the corresponding 'odd' distributions were created in response to this). This methodology meant that the odd individual observed by participants in experimental trials could exhibit less, or (crucially) more complex (and therefore, more likely effective) protean movement than the conformist individuals in its grouping (See Fig. 5.4). I was therefore able to isolate behavioural oddity of movement and saw that odd individuals were significantly more likely to be targeted with increased accuracy, regardless of the 'quality' of their protean movement paths. This finding highlights the apparently contradictory selection pressures present in animal groupings, i.e. maintaining sufficient similarity of movement with respect to groupmates (i.e. with respect to size, colouration, activity levels etc. [Blakeslee et al., 2009; McRobert & Bradner, 1998; Pritchard, Lawrence, Butlin, & Krause, 2001; Ranta, Lindström, & Peuhkuri, 1992; Rodgers et al., 2011]), whilst also displaying sufficiently unpredictable protean movements to avoid the threat of predation (Godin, 1986; Jones et al., 2011). For example, if an individual within a group displayed a novel protean strategy that was more effective than the strategies of other group members, our result implies that the emerging strategy would be preferentially and more accurately targeted (key determinants of successful predation [Olberg, Worthington, & Venator, 2000]). Therefore, in order for an effective novel protean

strategy to emerge within a group, an individual's novel behaviour will have to overcome the detriment of the oddity effect in order to gain a net benefit. However, while some phenotypic components that can result in an oddity effect (e.g. colouration) have a degree of plasticity, behaviour is considered far more plastic and can change rapidly (and reversibly), particularly in response to predation pressure (Orizaola, Dahl, & Laurila, 2012). This plasticity could allow the rapid adoption of a more successful strategy of anti-predator movement throughout the group to the point where the oddity effect would diminish and disappear (see Landeau & Terborgh, 1986) resulting in a further benefit for the grouping.

In summary, the primary conclusion I can draw from this study is that anomalous protean behaviour can induce an oddity effect resulting in the preferential and more accurate targeting of the odd individual. Here I have shown that protean behaviour, which by definition consists of unpredictable elements from the perspective of a predator, cannot be perceptibly different from its group mates without risking preferential targeting. Furthermore, a novel protean movement is targeted preferentially and with greater accuracy regardless of the movements' difference in complexity (an indicator of efficacy) relative to the group. From this result I have inferred that emergent protean strategies within groups would have to overcome the oddity effect in order to provide a net benefit for the individual and perhaps become the dominant protean strategy within the group. This would allow the group's overall movement to remain similar, while allowing the most effective protean strategies to evolve. Our results provide further insight into the nature of anti-predator movements with respect to the selection pressures that exist among group living organisms. In addition, I have suggested a possible mechanism by which

protean behavioural strategies may evolve within animal groupings. The emergence of protean movements on an individual basis in response to the selection pressures of predation is explored in chapter six.

6. Exploring Protean Movement with a Human Performance-Based Genetic Algorithm

6.1 Chapter Abstract

Behaviours evolve relatively rapidly within populations. As predation pressure is a critical agent in the natural selection of prey populations, anti-predator behaviours, including protean movements, are no exception. In this thesis, literature values or data from pilot studies were used to define the protean movement characteristics of digital prey items. While wide variation of protean movement path values has been expressed, the effectiveness resulting from the varying strategies displayed was not necessarily the subject of the study and did not allow for a comprehensive exploration into why certain combinations were more or less protean (with respect to their ability to evade targeting). In order to more fully explore how the characteristics of movement can interact to result in effective protean movement strategies, a novel genetic algorithm (GA) was created and implemented. This GA allowed effective protean movement stratagem(s) to develop in response to selection pressure from human participants targeting digital prey items in VR. Here I have shown that protean strategies that result from the GA conform to certain principles of protean movement previously explored while also establishing a significant effect of turn frequency which had previously resulted in non-significant effects with regards to predicting targeting difficulty. The results of this study indicate the existence of a general evolutionary trend within this predator-prey context, which all independent runs of protean behavioural genotypes tended towards.

Furthermore, the GA developed and implemented here may also provide an interesting avenue for further research into protean movement in varying contexts of predator-prey interaction.

6.2 Introduction

Predation pressure forms a key agent of natural selection in prey populations, typically via the selective targeting by predators on specific classes of prey items (Endler, 1986; Wade & Kalisz, 1990). This pressure results in the development of a wide range of adaptations that can improve the survivability of prey items (Edmunds, 1974). While certain adaptations such as chemical defences are iterative and may take many millions of years to evolve (Rodrigues, Andelman, & Bakarr, 2004), the evolution of behaviour (including anti-predator behaviour) is relatively quick and population level changes can take place in much shorter time scales (e.g. < 1000 years [Beauchamp, 2004; Blumstein, 2002; Magurran, Seghers, Carvalho, & Shaw, 1992; Massaro, Starling-Windhof, Briskie, & Martin, 2008]). Furthermore, the phenotypic plasticity of behaviour (often considered the 'most plastic' phenotype [Briffa, Rundle, & Fryer, 2008; Chapman, Ward, & Krause, 2008]) can facilitate rapid (and reversible) intra-generational behavioural changes, in response to changing environmental factors such as resource availability, disease prevalence, and predation pressure (Candolin, Wong, & Wong, 2012; Orizaola et al., 2012). Both rapid evolution and phenotypic plasticity may therefore facilitate the increasing effectiveness of protean anti-predator movements in response to predation pressure. However, the complexities of the interactions make quantifying the impacts of individual selection

pressures (i.e. predation pressure) on population level behavioural change difficult with traditional methods (i.e. mathematical modelling).

Mathematical modelling in biosciences represents the most commonly used tool in the field to describe, explain or predict observed phenomena from the natural world and remains an integral part of the field of behavioural ecology (Hamblin, 2013; Krebs & Davies, 1981; Ruxton & Beauchamp, 2008). However, as the relationships among independent variables are refined, the complexity of models inevitably increases (Hamblin, 2013; Ruxton & Beauchamp, 2008). Finding analytic solutions to complex models is challenging and even seemingly simple questions can lead to models which are intractable analytically (e.g. Beck, Shapiro, Choksi, & Promislow, 2002; Vrugt & Robinson, 2007). Using protean movement strategies as an example, an effective strategy with respect to avoiding predation is a function of not only an individual's movement behaviour, but may also include confounds such as the context of the interaction (i.e. ambush vs pursuit), the presence of other individuals (predators or prey) and the variation in strategies utilised by conspecifics. An effective strategy for one set of circumstances may therefore be ineffective if some or all of the aforementioned confounds vary. For example, when near a simulated predatory threat, Pacific blue eyes (*Pseudomugil signifer*) respond with increased complexity in their movement patterns (indicative of more effective protean movement [Richardson et al., 2018]), whereas a more distant threat does not illicit increased movement complexity (Herbert-Read et al., 2017). In order to systematically evaluate the effectiveness of protean movement strategies that an animal may express, these confounds must be finely controlled, but even so, a full exploration of the characteristics of movement and their relationship with effective

protean movement may result in intractable models when using traditional techniques.

Various observations of protean movement have shown that the individual characteristics of flight can contribute to effectiveness of protean movement strategies. For example, faster animals are harder to capture (Van Damme & Van Dooren, 1999), but some protean movement paths consist of the animal stopping completely before resuming movement, thereby interrupting the predicted interception point and purportedly making prey capture more difficult for predators (Edut & Eilam, 2004). Alternatively, animals moving in protean paths may reduce their speed periodically, which in addition to increasing unpredictability, may facilitate more extreme turns (Herbert-Read et al., 2015; Wilson et al., 2013). Furthermore, several animal species may show a variety of preferred escape trajectories, which may make predicting the direction in which the animal moves more difficult for predators (Paolo Domenici et al., 2008; Eifler & Eifler, 2014). Additionally, the timing of turns (regardless of the angle turned) can result in successful evasion of predators (Combes et al., 2012). This evidence demonstrates that all components of animal's movement can show variation which may increase the effectiveness of protean movement and reduce the chances of capture. However, with the exception of the study by Combes et al. (2012), the increases in unpredictability constitute indirect evidence that protean movement increases the difficulty of capture by predators and do not examine how the characteristics of movement may interact and combine to result in effective protean movement strategies.

Over the course of this thesis, I have used a variety of values to define the protean movement characteristics of digital prey items. Literature values were used wherever possible and data from pilot studies if not. While several methods I utilised have allowed wide variation in the values expressed (particularly in chapters four and five), the effectiveness resulting from the varying strategies displayed was not necessarily the subject of the study (i.e. chapters four and five examined the effects of group size and oddity respectively on protean movement) and did not allow for a comprehensive exploration into why certain combinations were more or less protean (with respect to their ability to evade targeting). I therefore wanted to more fully explore how the characteristics of movement can interact to result in effective protean movement strategies. To do so, I created a novel genetic algorithm (GA) which allowed effective protean movement stratagem(s) to develop in response to selection pressure from human participants.

A GA is type of evolutionary algorithm that modifies a 'population' of candidate solutions to a given problem, using 'bio-operators' inspired by natural genetic variation and natural selection (Mitchell, 1999). GA's were first described by Holland (1975) and have since been applied in a wide range of fields including mathematics, engineering, computer science, economics and bioscience (Arifovic, 1994; Del Moral, Hu, & Wu, 2010; dos-Santos-Paulino, Nebel, & Flórez-Revuelta, 2014; Hill, Lundgren, Fredriksson, & Schiöth, 2005; Li, Ng, Murray-Smith, Gray, & Sharman, 1996). Furthermore, in recent years the use of GA's in behavioural ecology has grown in popularity, where they have been used to examine a number of problems including group foraging using the producer-scrounger model ('selfish foraging') (Barta et al., 1997; He et al., 2006), vertical migration in planktivorous fish

(Huse et al., 1999) and anti-predator vigilance (Ruxton & Beauchamp, 2008). Additionally, French (2010) utilised a genetic algorithm and simulated predators and prey to study population-level variation of protean movement paths between sexual and asexual reproduction. To elaborate, French (2010) concluded that the optimal escape strategy from the prey's standpoint would be to have a small number of highly reflexive, largely innate (and, therefore, very fast) escape patterns, but that would also be unlearnable by the predator. Furthermore, it was concluded that the diversity inherent escape movements was increased as a result of sexual reproduction in comparison to asexual reproduction. However, as the qualities of the escape paths were not the primary focus of the study, the two-dimensional protean movement patterns moved at a constant speed only varied in one aspect of their movement (the angle and timing of the turns of a two-dimensional protean path). The study did not examine how continuous variation in speed interacts to make an example of protean movement effective.

GA's as described by Holland (1974) act upon data (as opposed to nucleotides in evolutionary processes), with the innovators (agents of genetic change [e.g. mutation or chromosomal crossover]) and selectors (agents that decides fitness in the system [e.g. natural selection, selective breeding]) being computational processes. The method is therefore entirely in silico. Fitness evaluations in this case were represented by how effectively a digital predator 'chased' the digital prey. However, there have been several variant forms of genetic algorithms that have been created which involve innovators and selectors that are not computationally based. Human-based Genetic Algorithms (HBGA) were first described by Kosorukoff, (2001) and removed the computation elements of a classic GA in favour of utilising humans

at every stage of the GA as initialisers (i.e. outlining the problem and initialising the first generation of solutions), selectors and innovators. An example of this would be 'crowd-sourced' solutions to a problem posed by another human, as in Community-based Question Answering (CQA) services such as Yahoo!™ Answers, Quora™ and Stack Exchange™ (Dror, Pelleg, Rokhlenko, & Szpektor, 2012). If a GA is analogous to natural selection, a HBGA is analogous to genetic engineering. Finally, Interactive Genetic Algorithms (IGA) contain both computation and human evaluation as innovators and selectors respectively (i.e. solutions are generated by computational processes and evaluated for fitness by humans). IGA's were first described by Dawkins (1986) and are useful in situations where the evaluation criteria are more subjective. For example, evaluating the attractiveness of images of individuals, or the aesthetic qualities of music, art and fashion (Cho, 2002; Gong, Yuan, & Sun, 2011; Johnston & Franklin, 1993; Tokui & Iba, 2000; Wong, Karimi, Devcic, McLaren, & Chen, 2008). In this chapter, a novel IGA was used to explore the emergence of effective protean movement.

While the fitness criteria in IGA's are typically subjective, I have demonstrated in previous chapters that the effectiveness of a protean movement paths can be quantified via the ability of a human 'predators' to target a digital prey item (a key determinant of successful predation [Olberg, Worthington, & Venator, 2000]). I therefore utilised this objective criterion as a fitness assessor in a novel GA that I have termed a Human Performance-based Genetic Algorithm (HPBGA). This will cause the protean movement paths of prey to increase in effectiveness with respect to their ability to evade human participants acting as 'predators'.

The overarching aim of this chapter was to examine the emergence of effective protean movement and compare successful, evolved protean movements to 'control' evolutions not directed by human performance. Firstly, I hypothesised that the fitness of experimental evolutions would differ significantly than that of control evolutions. Specifically, I predicted that movement paths from experimental evolutions would be significantly more difficult to target than movement paths from control evolutions. Secondly, I hypothesised that the complexity (entropy) of movement paths would differ significantly between experimental and control evolutions with the prediction that movement path complexity would be significantly higher in paths derived from experimental evolutions. Finally, I hypothesised that the flight characteristics of effective protean movements that emerged in experimental evolutions would differ significantly from the flight characteristics of control evolutions. Specifically, I predicted that the speeds of experimentally evolved movement paths would be significantly higher, with narrower variance than those of control evolutions. I also predicted that the turn angles of experimentally evolved movement paths would be significantly higher, with wider variance than those of control evolutions. Finally, I predicted that the time between turns for experimentally evolved movement paths would be significantly lower, with a wider variance than those of control evolutions.

6.3 Materials & Methods

6.3.1 Simulations

Similar to chapter two (Richardson et al., 2018), simulations were created in the Unity3D game engine running on a Microsoft Windows PC, and built to run on a

Samsung Galaxy S7 smartphone using the Samsung Gear VR system. Simulation design, appearance and function was also similar to previous chapters.

Simulations consisted of a black sphere (the 'prey') presented against a homogenous white background to maximise contrast. The prey moved in a 3D virtual space centred on a point directly in front of the participant. The prey items began each trial directly in front of the participant at a distance of 19 m and subtended a visual angle of $\pi/60$ radians. Within the simulation, participants were free to look around the virtual environment. A small, red circle (the reticle) was superimposed onto the centre of the participants' field of view and provided a point of reference for the participant to facilitate targeting, allowing them to interact with the moving prey item in real time. Participants were tasked with targeting the prey item as accurately as possible within the VR simulation.

6.3.2   Prey movement

Prey movement used principles similar to those of chapters four and five, namely a series of digital 'genotypes' (probability mass functions) from which movement paths could be drawn. The movement paths themselves consisted of a series of steps during each of which a prey item travelled in a straight line in 3D space before turning and moving off on a different trajectory. Movement of prey in the simulation was determined by three parameters: the speed at which the prey moves within the virtual environment in metres per second (hereafter referred to as 'speed'), the angle in degrees turned within a cone centred on the prey's direction of travel (hereafter termed 'angle') and the time in seconds until the next turn (hereafter termed 'time').

The next step was to decide the parameter space of the prey items movement characteristics. I chose a maximum speed of 4.65 ms^{-1} which was derived from the median value of the animal speed database compiled by Hirt et al. (2017) [supplementary material]. Our speed range was therefore between 0 ms^{-1} and 4.65 ms^{-1}. The angle search space constrained the widest possible turn to 90° ($\pi/2$ radians), thereby putting the range of angle values between 0 and $\pi/2$ radians. Finally, for the time characteristic, the maximum value was decided based on the length of each trial, which was three seconds. Three second trials were chosen as this allowed a large variation of protean movement paths to be expressed while also not allowing the prey item to move out of the comfortable range of motion of a participants head movements (even when travelling at maximum speed in a straight line). The lower value was based on the frame rate of the simulation (displayed to the participant at 50Hz [also the frequency at which data was recorded]). This put the range of time values from 0.02 s to 3 s.

The first generation of prey movement genotypes (hereafter referred to as 'starting genotypes') consisted of uniform distributions that were confined to 10% of their respective parameters' search space. For the speed starting genotype, these initial starting bounds were 2.09 to 2.56 ms^{-1}. For the time starting genotype, these initial starting bounds were 1.34 to 1.64 s. The aforementioned flight characteristics' starting values were roughly in the middle of their parameter space in order to allow genotype development toward either (or both) of the extremes. For the angle distribution, the starting bounds were 0 to $\pi/20$ radians. I chose to start the turn angle distribution centred on straight-forward trajectories. Thereby the initial starting genotypes will result in prey items moving directly (or nearly directly) away

from the predator. This allowed genotype development from an initial narrow set of turn angles. Using these values, I generated starting genotypes for the population (see below). Paths were generated from genotypes using the same method as described in chapter four.
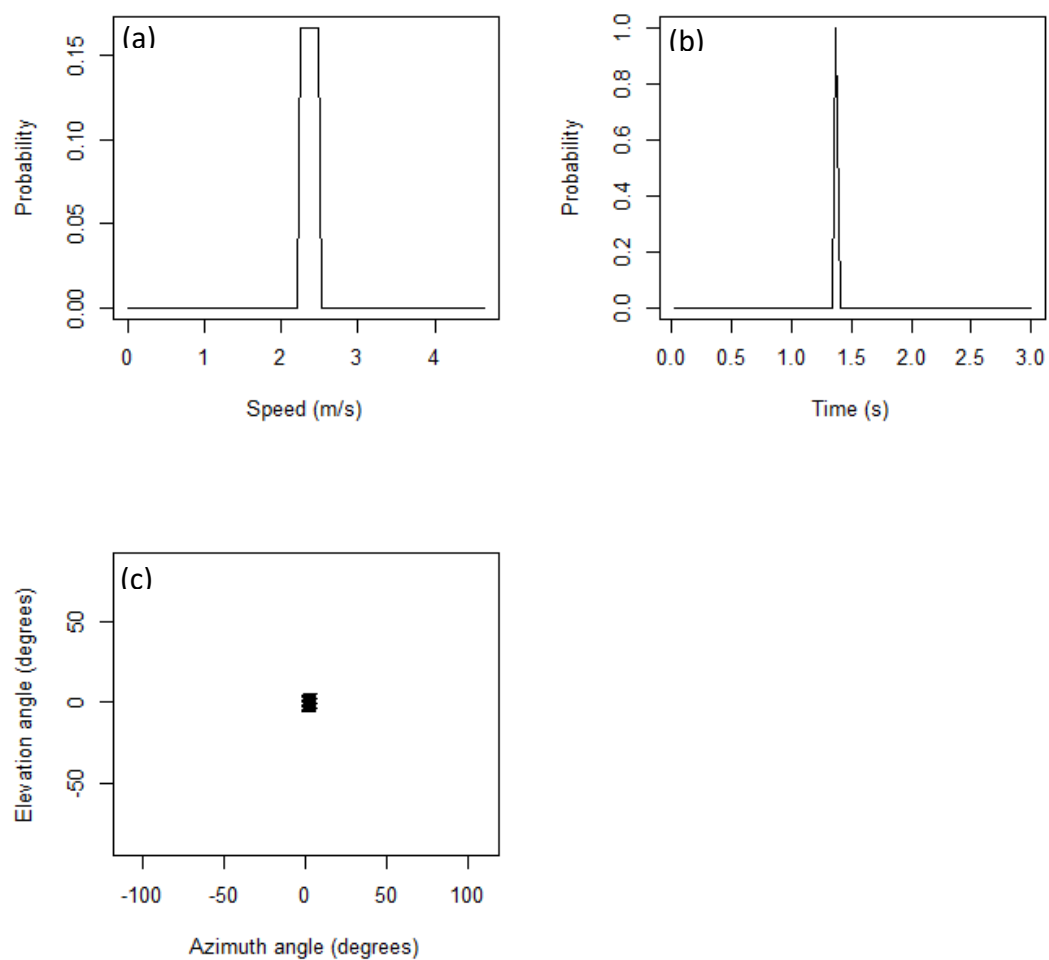
Fig. 6.2 Visualisation of a representative starting genotype: (a) speed, (b) time and (c) turn angle. Note that turn angle is represented in spherical coordinates (azimuth and elevation) with the dark areas representing the probability of those values being drawn from the genotype (darker = higher probability).

6.3.3 Structure of Human Performance-Based Genetic Algorithm

In a typical genetic algorithm, a 'population' of solutions (individual solutions are often referred to as a 'chromosomes') is generated. The fitness of individuals within the population are evaluated, and the fitness function is used to calculate the overall quality of the solution with respect to the problem (Mitchell, 1999). If the threshold for fitness is not exceeded, the individuals of the population are subjected to a series of functions that mimic biological processes similar to natural selection. These can include selection (and/or elitism), crossover and mutation. Selection refers to ranking the solutions by their fitness with respect to the problem, with fitter individuals being more likely to carry over to the next iteration of the algorithm (usually referred to as a 'generation'). Elitism occurs when a proportion of the fittest individuals is carried over to the next generation unmodified (De Jong, 1975). Fitter individuals are then selected as 'parents' to generate new solutions. There is then a chance that crossover can occur between parents to create 'offspring'. In a crossover, the parent genotypes are crossed over in a manner analogous to a chromosomal crossover during sexual reproduction (Holland, 1975). Parts of the solution are randomly swapped between parents to produce an entirely different solution that was derived from relatively fit individuals. Due to the randomised nature of the crossover, the parental contribution to the new solution may be unequal (i.e. one 'parent' may contribute more of their genotype to their offspring than the other). Once the crossovers have occurred, the population may be mutated. Mutations are primarily introduced in order to prevent the GA stalling at local optima by maintain the diversity of available solutions (Da Ronco & Benini, 2014). There are a variety of methods of mutation that have been used in GA's. Most often it is analogous to a point mutation in a DNA or RNA

sequence. For example, if a chromosome is represented by a binary string, a mutation may take the form of a single flipped bit from a one to a zero or vice versa. These processes ultimately result in the next generation population of chromosomes that is different from the preceding generation. Furthermore, in general as a result of the aforementioned processes, the average fitness of the population should increase, since only the best organisms from the first generation are selected for breeding, along with a small proportion of less fit solutions. These less fit solutions are included to ensure genetic diversity of potential solutions within the gene pool of the parents and therefore ensure the genetic diversity of the subsequent generation of offspring (Mitchell, 1999).

The genotypes described above were the information that was modified by the genetic algorithm. A population was comprised of 20 genotypes that were evaluated by human participants. In order to evaluate the fitness of a genotype, five paths were randomly generated from the genotypes (see chapter 4) and displayed in the VR simulation. The mean distance (in m) of the participants gaze to the prey item over each three second trial described the fitness of an individual path. The overall fitness of the genotype was calculated as the median fitness value for the five path fitness evaluations. Once five paths from each genotype in the population had been observed (and therefore the fitness of each genotype evaluated), the genetic algorithm would operate on the population. Fig.6.2 visualises this process.
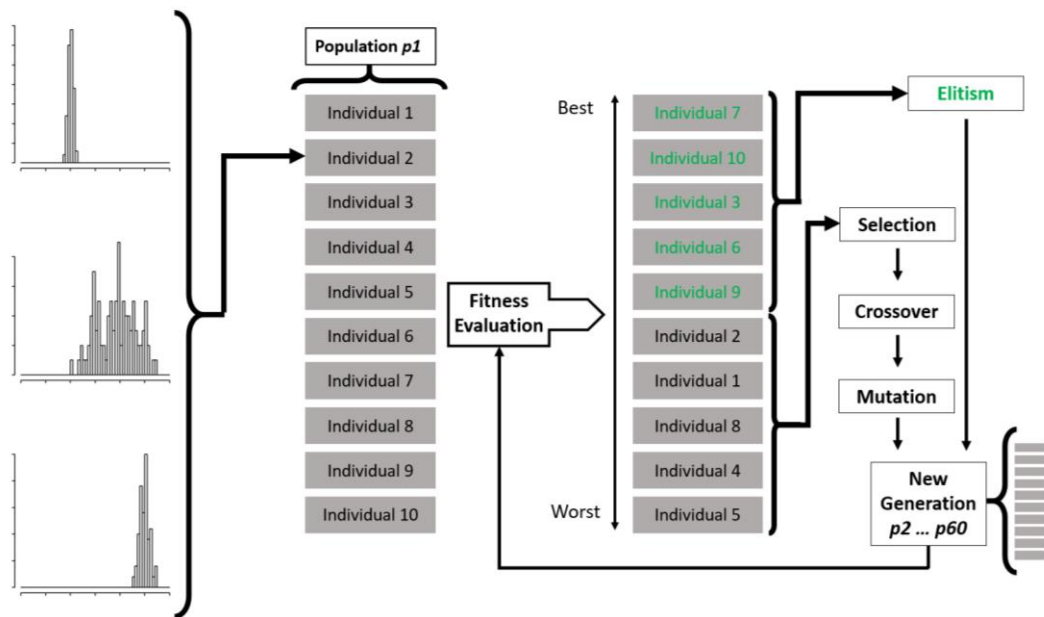
Fig. 6.4 Overview of the structure of the genetic algorithm used here. The left three figures represent three probability distributions that comprise the genotype of a single individual. The population is evaluated and ranked by fitness. Bio operators are applied. A new generation of modified genotypes is derived. The process repeats until 60 generations have been evaluated. Note that the population size depicted here is for illustrative purposes only. Experimental evolution population size was 20.

Firstly, the genotypes were ranked on their fitness from highest to lowest. Then, an elitism function would select the top 50% of the population with respect to fitness. These elites would carry over to the next generation unmodified. By retaining solutions that are known to be effective, if crossovers or mutations (see below) result in offspring that are weaker than the parents, the original fitter solutions will not be lost (Mitchell, 1999). Furthermore, high elitism proportions (as used here) can also speed the rate at which the GA finds effective solutions (i.e. a fewer number of iterations is needed) (Rani, Suri, & Goyal, 2019; Yannakakis, Levine, & Hallam, 2004). This was relevant in this study, which required a large number of human participants to drive the behavioural evolution. Next, the population (both elites and the remainder) were selected to produce 'child' genotypes. Weighted probabilities were calculated via min-max scaling and assigned to each genotype. Two 'parent'

genotypes were selected via sampling based on the weighted probabilities with fitter individuals therefore more likely to be selected and reproduce. From these parent genotypes, the crossover bio operator was then individually applied to the speed, time and angle probability density functions within each genotype. In a crossover, each probability density function of the parent genotypes were combined according to a weighted average to produce a child genotype. Specifically, a random value between zero and one (w_1) was generated for one parent as a weighted probability. The weighted probability for the second parent (w_2) was then calculated based on the first value ($w_2 = 1 - w_1$). The two parent genotypes were then combined and averaged according to their weighting. This meant that each parent contributed a random percentage of their genotype (summing to 100%) to produce a child genotype. The resultant child genotype would therefore be a random combination of the two parent genotypes (which would likely, but not necessarily be the most fit individuals). This probability of a crossover occurring was set to 80%. A high value was chosen to ensure effective genotypes propagated through populations rapidly (Holland, 1975; Mitchell, 1999).

Next, the mutation bio operator was applied to the child genotypes. The mutation operation shifted the entire probability mass function of each flight characteristic a small distance toward one of the extremes (with respect to the search space of each flight characteristic). The shift in each probability mass function was based on a number drawn from a normal distribution with a mean of zero and a standard deviation equal to the starting bounds of the corresponding flight characteristic (see above [prey movement]). The relatively narrow standard deviation and the normal distribution meant that a single mutation was unlikely to

result in a large shift of the probability distribution it was acting upon. However, I also had the mutation probability set to 100% so that the flight characteristic probability mass functions shifted at every opportunity and variation was introduced in all offspring, rather than the more conventional use of large, infrequent events (Da Ronco & Benini, 2014). Following the application of the bio operators, the new set of genotypes was considered the next generation, whereupon the fitness was evaluated again. This process continued until 60 generations had been fully evaluated. This number of generations was chosen after pilot studies showed a tendency for fitness to plateau before 60 generations.

In order to more fully explore the parameter space and potential protean movement strategies that could emerge, I created six separate populations of starting genotypes. The GA operated independently on each of these separate populations. Each separate population was referred to as a 'run', with six runs in total being completed (see Table 6.1 for clarification). While the runs were independent of one another, each run occurred concurrently. To clarify, only one human participant could evaluate the fitness of the movement paths at a time, but they were equally likely to see paths from any of the six separate runs as the order of trials was randomised.

In addition to the six runs of experimental evolutions, I also created 'control' runs. To elaborate, in control runs, the process was entirely in silico and, unlike experimental evolutions, human performance was not used to assess the fitness of flight paths for the GA. Instead, the fitness of each genotype was decided based on random number generation. Human participants tested the first and 60th

generations of generated paths of control evolutions (see 'experimental protocol' for more details), but the targeting accuracy values were not used to derive fitness in control evolutions of the GA (unlike experimental evolutions). The purpose of the control runs was to provide comparisons between the movement patterns developed with and without human performance-based selection pressure. The differences between experimental and control evolutions would help determine the characteristics that make protean movement effective and replicate genetic drift (the change in the frequency of existing genotypes in a population due to random sampling of organisms) in a randomly selected population. As the in-silico control runs assigned randomised fitness values to genotypes (as opposed to assessing movement paths), movement paths were only generated upon request. As I was not investigating the progression of the 'genetic drift' represented by the control evolutions, but the differences in movement path characteristics (and the corresponding impact on targeting accuracy) with and without human-performance based evaluations, comparisons between human performance in experimental and control evolutions were only made between generation one and generation 60, where the experimental evolutions would likely have the highest fitness. Note however that the entropy data and flight characteristics were available for all control and experimental runs. Additionally, control evolutions were all derived from the same starting populations of genotypes from an experimental run.

Table 6.1 A breakdown of the different tiers that encompass the total trial figure (listed at the bottom)

Tier	Frequency
Runs	6
Generations per run	60
Individuals per generation	20
Path assessments per individual	5
Total trials	36,000

6.3.4 *Experimental protocol*

A total of $n = 432$ participants took part in this study. Of these, 392 participated in evaluating fitness for the experimental runs (218 females, 175 males; mean age = 22.8 [range, 18 – 55]) and 40 participated in evaluating fitness for the control runs (23 females, 17 males; mean age = 23.9 [range, 20 – 33]). All participants were staff or students at the University of Lincoln. Before providing consent to take part in the study, participants were given written information on the general aims of the study (although not the specific hypotheses being tested), what they would be asked to do, and the approximate time required to complete the study. Their age and gender were reported (but not linked to their experimental data). This project was approved by the College of Science ethics committee at the University of Lincoln (reference CoSREC265). After consent was given, a detailed verbal briefing was given to each participant to ensure they understood their role in the data collection.

The participants were instructed on the use of VR headset, including fitting and focus adjustment. As per the experimental protocol detailed in chapter two, participants were instructed that their task was to constantly target the prey item with the reticle as accurately as possible as it moved around the virtual environment. To start each trial, the participant used their head movements to position the reticle

over the black sphere representing the prey item. When the reticle was over the prey item, a visual countdown object indicated that the trial would start in one second (the trial would only begin if the reticle was over the prey item for a full second). After this, the countdown indicator would disappear, and the trial would begin. Each trial lasted 3 s. In the experimental evolutions, participants were instructed that they could take part in as many, or as few trials as they wished. However, the experimenter did suggest at least 50 trials per participant. In control evolutions, as there were a fixed number of trials per participant, participants were instructed that there would be 33 trials in total (three training trials [see below] plus 30 experimental trials). This was the only difference in experimental protocol between experimental and control evolutions. All participants were also permitted to take breaks or stop completely at any time, for any reason. Before the experimental trials began, participants viewed three 'training trials' in order to familiarise themselves with object targeting. The movement characteristics of each training trial got progressively more extreme (i.e. higher speed and angle values, with lower time values) with each trial so the participant could acclimate to object targeting in VR and familiarise themselves with the types of movement patterns they would be observing before they started contributing to the selection process.

Once the training trials were completed, the experimental testing trials began. Each trial presented the participant with a single prey item that was positioned at the starting coordinates (18.95 m in front of the participant). After the visual countdown indicator, the prey items would begin moving according to their flight paths. For all trials, each participant was instructed that they were to target the prey item as accurately as they could. The order of experimental trials (i.e. the

individual and replicate number of the current generation) was randomized for each participant.

6.3.5 Data collection

Telemetry data of the participant's head orientation (a 3D vector passing through a point between the participant's eyes and towards the reticle) were collected every 0.02 s throughout each trial. At the end of each trial, the telemetry data recorded by the VR device was sent to a networked Microsoft Windows PC. The PC hosted a server written in R that was responsible for serving flight paths to the VR device, receiving fitness evaluations for each path and running iterations of the genetic algorithm once all data for a generation was received and processed. For experimental evolutions, each genotype, flight path and corresponding telemetry data from every trial was recorded to the PC to be used for analysis. However, for fitness evaluations of flight paths derived from control evolutions, the paths were pre-loaded onto the device as text files, with telemetry being recorded to the smartphone and exported to a PC in an identical manner as with chapters two, four and five.

6.3.6 Statistical analysis

Analyses were conducted using general linear mixed-effects models (glmm) in R version 3.5.2, using the lmer function in the lme4 package (Bates et al., 2015). The validity of the model assumptions was confirmed by visually assessing the normality of the model residuals.

Firstly, I tested whether the fitness of experimental evolutions increased over generational time. I included mean targeting accuracy of each movement path (representing a 'fitness' evaluation) as the dependent variable. The generation number of the individual were used as a continuous predictor. I included each participant's anonymous identifier as a covariate to control for varying aptitudes for object targeting between participants. I also included the run number, individual number (i.e. which of the 20 genotypes [population] the path was drawn from) and replicate as random effects to control for repeated viewings of movement paths derived from the same run or genotype. Significance was determined by comparing the full model to a reduced model lacking the term of interest using a likelihood ratio test (Crawley, 2005). I then compared the fitness of experimental evolutions to control evolutions. Specifically, I tested whether evolution type (i.e. experimental or control) and generation number predicted the fitness of protean movement paths. As the fitness of control evolutions was only evaluated at generations one and 60, only generations one and 60 (both control and experimental) were included in this analysis. I included fitness of each movement path (mean targeting accuracy) as the dependent variable. The condition (i.e. experimental or control) and generation (one or 60) of the individual were used as categorical predictors and an interaction was fitted between these predictors. I included each participant's anonymous identifier as a covariate to control for varying aptitudes for object targeting between participants. I also included the same random effects as above. Significance was determined by comparing the full model to a reduced model lacking the term of interest using a likelihood ratio test (Crawley, 2005).

Next, I tested whether evolution type (i.e. experimental or control) and generation number predicted the complexity (entropy) of protean movement paths. Movement paths were drawn from control genotypes (five per individual, per generation) and the complexity (Shannon entropy, as defined in chapter two) of these paths was calculated. I included the entropy of each movement path as the dependent variable. The evolution type (i.e. experimental or control) and generation number of the individual were used as categorical predictors an interaction was fitted between these predictors. I included the same covariates and random effects as the above model. Significance was determined by comparing the full model to a reduced model lacking the term of interest using a likelihood ratio test (Crawley, 2005).

I then tested whether evolution type (i.e. experimental or control) and generation number predicted the values of the flight characteristic of protean movement paths. As the fitness of control evolutions was only evaluated at generations one and 60, only generations one and 60 (both control and experimental) were included in this analysis. I included the values of flight characteristics for each movement path as the dependent variable in three separate models (as the characteristics were affected by bio-operators independently)**.** The evolution type (i.e. experimental or control) and generation of the individual (one or 60) were used as categorical predictors. I included the same covariates and random effects as the above model. Significance was determined by comparing the full model to a reduced model lacking the term of interest using a likelihood ratio test (Crawley, 2005). I also examined the difference in variance between the experimental and control evolution flight characteristics. The normality of the generation 60 data was assessed visually using Q-Q plots. If both distributions were not normally distributed

a Fligner-Killeen test was used to test for differences in variance. Otherwise an F-test was used.

Finally, I visualised the similarity in the evolutionary trajectories of each run in comparison to controls by comparing the mean values of the flight characteristics of expressed paths to those of control paths over generational time. Full model outputs for all analyses are included in Appendix A.

6.4 Results

6.4.1 Targeting accuracy (fitness)

The targeting accuracy (i.e. 'fitness') of protean movement paths from the human performance-based genetic algorithm was significantly predicted by generation, with fitness (i.e. the overall mean distance from the participants gaze to the prey's centre) increasing over generational time (χ^2_1 = 6.39, *p* = 0.01; Fig.6.3). When looking at control and experimental targeting accuracy evaluations, I found that the targeting accuracy of the generated movement paths was significantly predicted by an interaction between evolution type (i.e. control or experimental) and generation number (χ^2_1 = 8.83, *p* = 0.003; Fig.6.4). Specifically, experimental evolutions at generation 60 had significantly higher targeting accuracy than control evolutions at generation 60. Additionally, generation number also significantly predicted targeting accuracy increase (χ^2_1 = 6.463, *p* = 0.01; Fig.6.4), with generation 60 targeting accuracy values being significantly higher than generation one targeting accuracy values, regardless of evolution type.
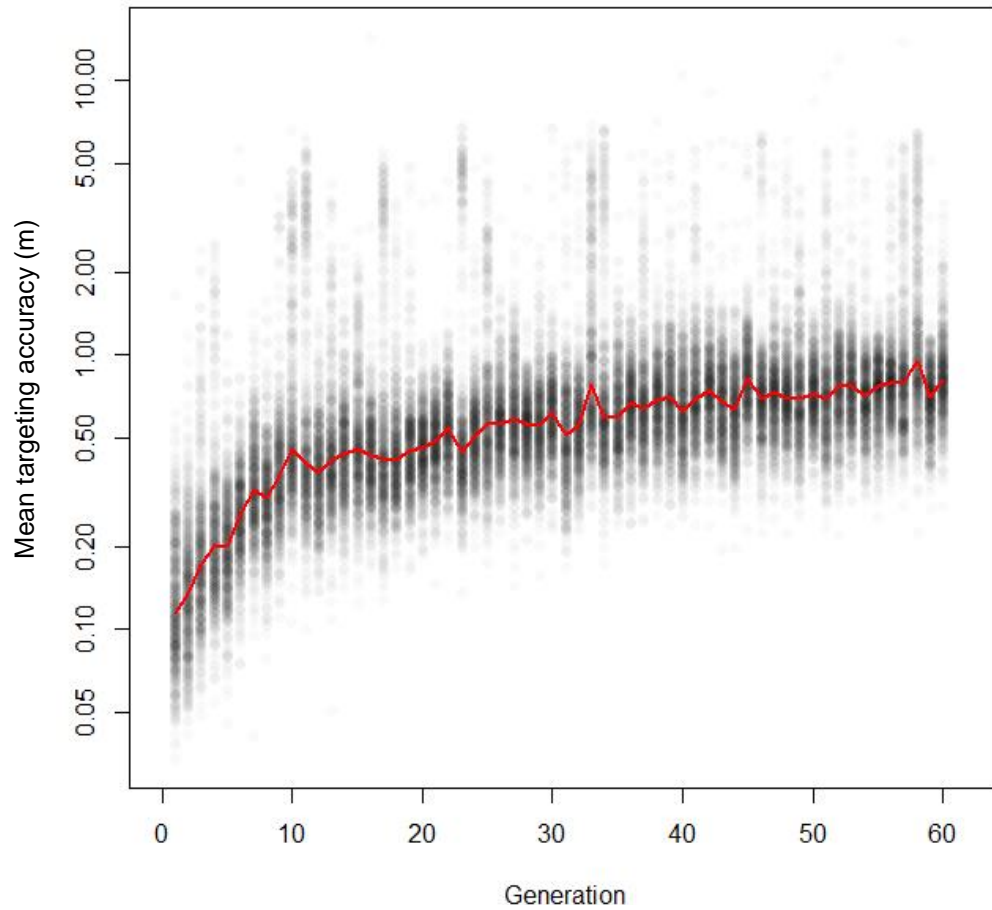
Fig. 6.7 Targeting accuracy, or 'Fitness' (measured as the mean distance from the centre of the prey item over each trial) for all individuals across all experimental generations. Higher values along the y-axis denote poorer targeting accuracy. Note the log scale on the y-axis. The red line denotes the population median targeting accuracy for each generation.
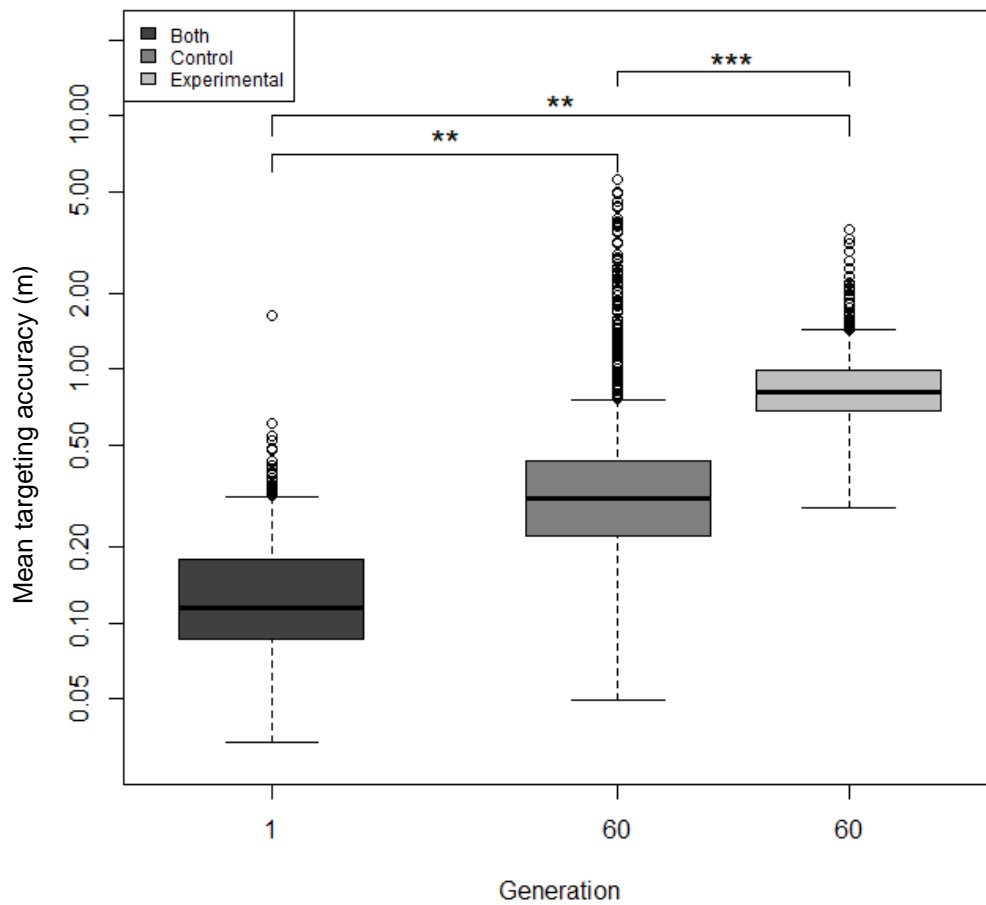
Fig. 6.8 Targeting accuracy, or 'Fitness' of the first and last generation in control and experimental evolutions respectively. Higher values along the y-axis denote poorer targeting accuracy. Note the log scale on the y-axis. Also note that since both control and experimental evolutions came from identical starting genotypes, only one box representing both evolution types is present. Asterisks denote significant differences (**, $p < 0.01$; ***, $p < 0.001$) between conditions.

6.4.2 Entropy

When looking at control and experimental protean movement path complexity, I found that the complexity (Shannon entropy) of the generated movement paths was significantly predicted by an interaction between evolution type (i.e. control or experimental) and generation number ($\chi_1^2 = 7283.23$, $p < 0.001$; Fig.6.5). Specifically, experimental evolutions showed significantly higher movement path complexity as generation increased than control evolutions at corresponding generations.

Additionally, increasing generations significantly predicted increasing complexity (χ^2_1 = 22600.21, $p < 0.001$; Fig.6.5), and experimental evolution path complexity showed higher complexity than control evolution path complexity (χ^2_1 = 22697.54, $p < 0.001$; Fig.6.5).
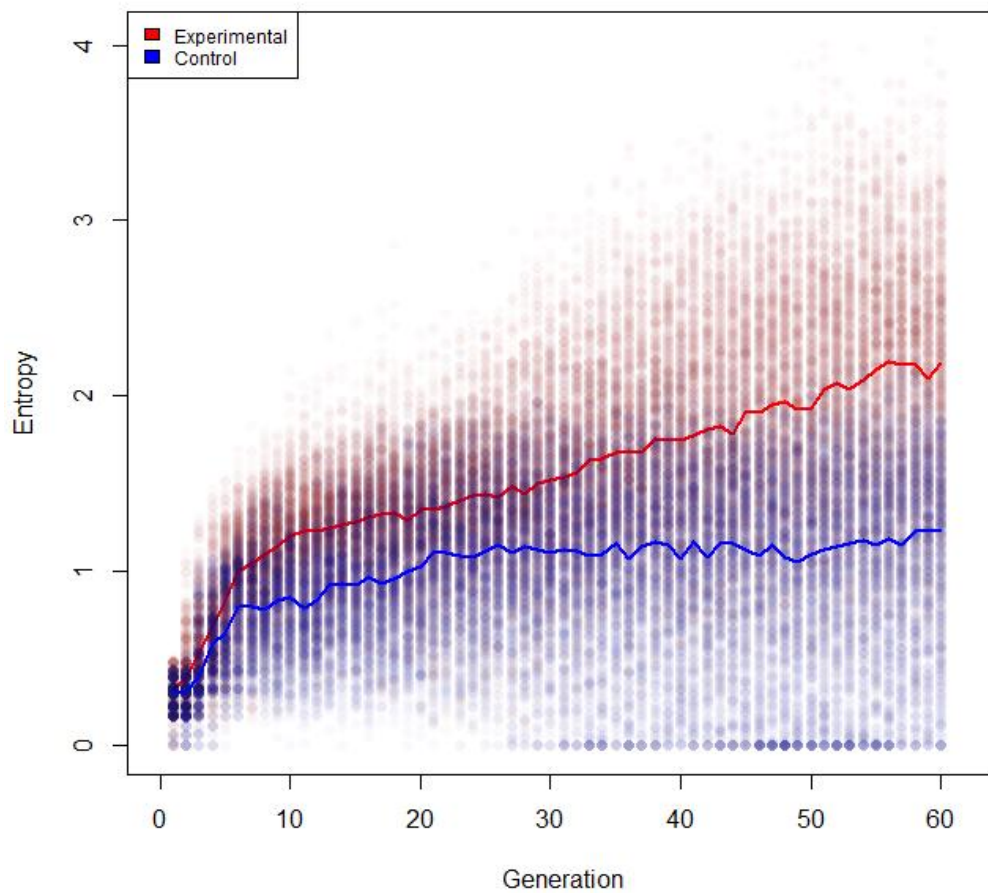
Fig. 6.9 Movement path entropy for experimental (red) and control (blue) individuals across all generations. Higher values along the y-axis denote increased complexity. The red line denotes the population median entropy score for experimental generations. The blue line denotes the population median entropy score for control generations.

6.4.3   Flight characteristics

Fig.6.6 visualises the change in flight characteristics of protean movement paths from the human performance-based genetic algorithm between the first and last generation for both control and experimental evolutions.

I found that the generation number and evolution type (i.e. control or experimental) significantly predicted the values of speed for the movement paths (χ^2_3 = 6733.44, p < 0.001; Fig. 6.6a). Specifically, movement path speeds were significantly greater in the final generation than the first generation for experimental evolutions and movement path speeds were significantly lower in the final generation than the first generation for control evolutions. Additionally, movement path speeds in the final generation of the experimental evolutions was significantly greater than that of the control evolutions. Furthermore, the variance of the speed values in control evolutions was significantly greater than the variance in experimental evolutions (Fligner-Killeen; χ^2 = 123.91, df = 53, p < 0.001).

I also found that the generation number and evolution type (i.e. control or experimental) significantly predicted the values of time between turns for the movement paths (χ^2_3 = 6151.81, p < 0.001; Fig. 6.6b). Specifically, movement path times were significantly lower in the final generation than the first generation for both control and experimental evolutions. Additionally, movement path values for time between turns in the final generation of the experimental evolutions was significantly lower than that of the control evolutions. Furthermore, the variance of the time values in control evolutions was significantly greater than the variance in experimental evolutions (Fligner-Killeen; χ^2 = 51.02, df = 38, p = 0.08).

Finally, I found that the generation number and evolution type (i.e. control or experimental) significantly predicted the values of turning angle for the movement paths (χ^2_3 = 4466.28, *p* < 0.001; Fig. 6.6c). Specifically, movement path turn angles were significantly higher in the final generation than the first generation for both control and experimental evolutions. Additionally, movement path values for turn angles in the final generation of the experimental evolutions was significantly higher than that of the control evolutions. Furthermore, the variance of the turn angle values in control evolutions showed no significant difference than the variance in experimental evolutions (Fligner-Killeen; χ^2 = 123.91, df = 52, *p* =0.54).
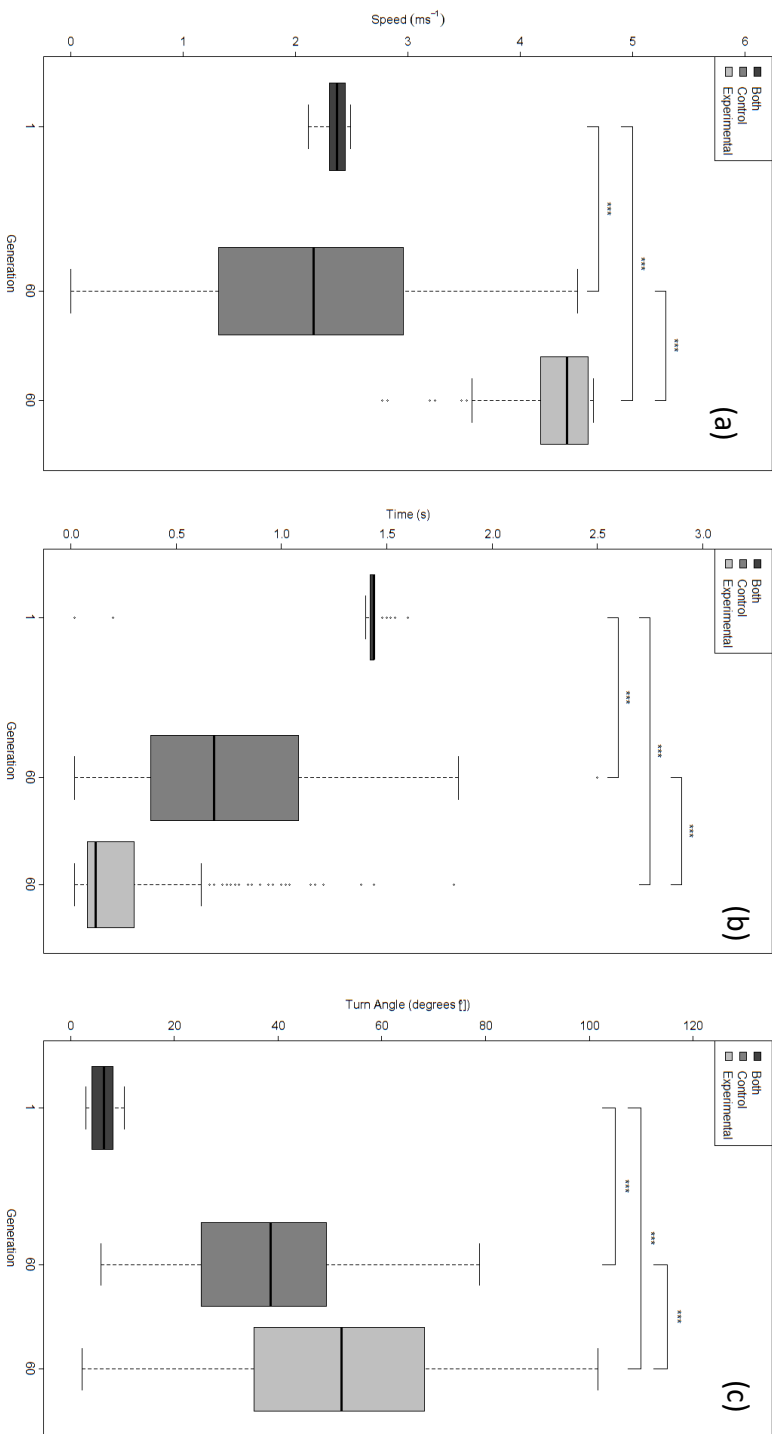
Fig. 6.13 Flight characteristics for the first and last generation in control and experimental evolutions respectively. Note that since both control and experimental evolutions came from identical starting genotypes, only one box representing both evolution types is present in each panel. Flight characteristics include (a) speed (in ms^{-1}), (b) time between turns (in seconds) and (c) turn angles (in degrees). Asterisks denote significant differences (***, p < 0.001) between conditions.

6.4.4 Evolutionary trajectory

Fig.6.7 visualises the overall similarity in the changing flight characteristics of protean movement paths over generational time. This indicates a generalised strategy represents the most effective protean movement in this predator-prey context.
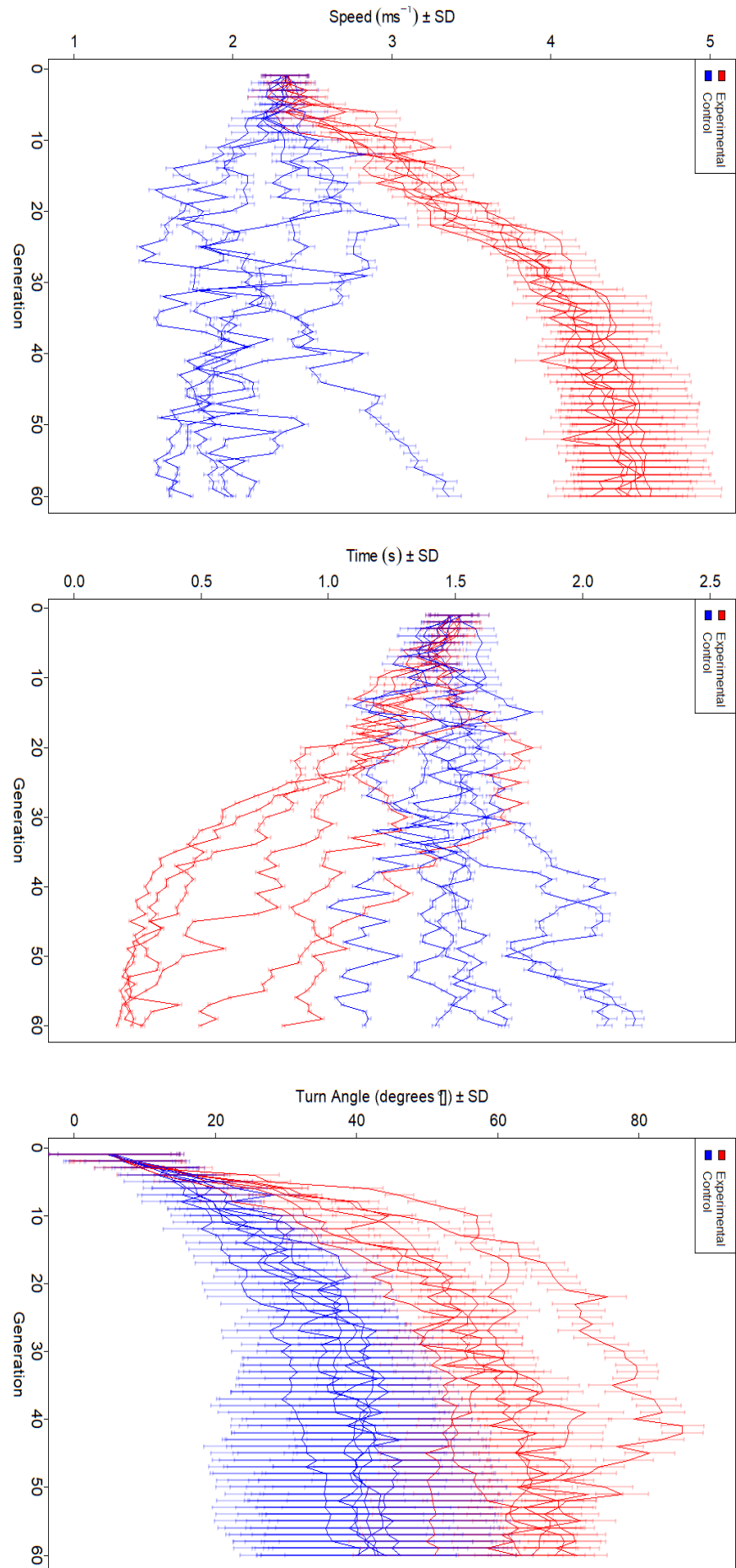
Fig. 6.15 Comparisons of mean flight characteristics values over generational time between all runs. Values for experimental (red) and control (blue) evolutions are fitted on each graph. Data from all runs are displayed and include standard deviation. (a) speed characteristic (ms⁻¹). (b) time characteristic (s). (c) turn angle (°).

6.5   Discussion

This study has given a number of insights into the development and expression of effective protean movement strategies. Firstly, I have shown that the novel GA used here has produced final generation protean movements that were significantly more effective at evading targeting by humans than the final generation protean movements derived from control evolutions (that were subject to randomised selection pressures). Additionally, the complexity (entropy) of protean movement paths from experimental evolutions increased over generational time. Moreover, the complexity of final generation experimental evolution protean movement paths was significantly greater than paths from control evolutions. Furthermore, all final generation flight characteristics were significantly different from those of control evolutions. Mean speed values for experimental evolutions showed a significant difference in variance from that of control speed values. The speed values for experimental evolutions had high median values with a narrow spread of data. Turn angle values for experimental evolutions showed no significant difference in variance from that of control turn angle values. The turn angle values for experimental evolutions and control evolutions both had a very wide spread that covered most of the search space, though the turn angle median values were significantly higher than that of the controls. Regarding time values, experimental evolutions showed a significant difference in variance from that of control time values. The time values for experimental evolutions had relatively low median values with a moderate spread of data. Finally, when combining all flight characteristics of all six runs into one distribution per generation, the evolution of all runs broadly followed the same evolutionary trajectory.

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In animal movement studies that have utilised GA's, the focus is typically on large scale processes such as migration (Huse & Giske, 1998; Li, Zhang, & Yin, 2014). The use of GA's at a spatiotemporal scale similar to that used here are most commonly seen in computer science when examining pathfinding optimisation in robotics (Choueiry, Owayjan, Diab, & Achkar, 2019; Sedighi, Ashenayi, Manikas, Wainwright, & Tai, 2004). While the optimisation selectors in these studies are different, applications of GA's in study of movement optimisation to a problem has nevertheless been established. Studies have investigated the adaptive movement of animals representative of individual predator-prey interactions (French, 2010) though, to my knowledge, no studies have utilised GA's to study movement paths representative of real animal movements (i.e. including variation in speed, turning angle and time between turns) as conducted here. The finding that protean movement can emerge from a parameter space based on real animal movements (as evidenced by the increasing fitness derived from human performance over generational time and significant differences between experimental and control fitness) demonstrates that GA's can form a useful analytical tool in the study of complicated movement strategies.

The fitness increase and significant difference from control evolutions (see Figs.6.3, 6.4) is mirrored in the complexity (entropy) of the paths produced at each generation (see Fig.6.5). Entropy of evolved experimental paths increased over generational time and was significantly more effective than control evolutions. This finding is in support of earlier general principles established regarding protean movement efficacy, specifically that increasing movement complexity is indicative of more effective protean movement (see chapter two; chapter three; Herbert-Read,

Ward, Sumpter, & Mann, 2015; Jones, Jackson, & Ruxton, 2011; Richardson et al., 2018). For future uses of GA's in the investigation of protean movement, it might seem sensible to suggest that the human element of the GA described here could be removed in favour of entropy (or some other measure of path complexity) allowing far more solutions to be tested quickly. However, while the relationship between protean movement and path complexity is a good general predictor of predator performance in this predator-prey context (see chapter two), a slight change in the predator-prey context may greatly affect the usefulness of entropy as a predictor of protean movement efficacy. To elaborate, the decision by a prey animal to engage (or not engage) in fleeing behaviour is based on a series of assessments and decisions which may be influenced by many factors. For example, the ability of prey to recognise predators (Coss & Ramakrishnan, 2000; Ferrari, Messier, & Chivers, 2008), the level of threat posed by the predator (Roi & Owings, 2010; Swaisgood, Owings, & Rowe, 1999), the distance between the predator and prey (Cooper & Frederick, 2007; Stankowich & Blumstein, 2005; Ydenberg & Dill, 1986) and environmental factors such as the availability of refuge (Ellard & Eller, 2009; Kramer & Bonenfant, 1997). All of these factors may affect both the decision of the prey to flee the predator and crucially, whether to incorporate protean movement into the fleeing behaviour (i.e. if a nearby refuge is available, a direct route to the refuge is the likely outcome upon detection of an imminent predatory threat [Kramer & Bonenfant, 1997]). For example, Herbert-Read et al., (2015) found that Pacific blue-eyes (*Pseudomugil signifer*) that were far away from a simulated predatory threat did not increase their movement path complexity, whereas those close to a threat did. This example illustrates that mathematical qualities of protean movement may be

inconsistent in their ability to predict protean movement efficacy between varying contexts of the predator-prey interaction. However, the use of humans as fitness evaluators in a GA as described here can be applied to a broad array of predator-prey contexts. For example, pursuit-evasion (i.e. having human predators pursue digital prey and 'strike' to directly capture individuals). The high degree of experimental control over the circumstances of the predator-prey interaction would allow deeper investigation into the qualities that result in contextually effective protean movements, thereby providing greater insight into the fine-scale processes of predator-prey interactions.

When observing the changes that took place in the control genotypes by generation 60 (see Figs. 6.4, 6.5), the control genotypes changed significantly with respect to their starting point. Interestingly, while the control evolutions were undirected by human performance, when the fitness of these solutions was evaluated by human participants at generation 60, fitness was significantly higher than that of generation one (but significantly lower than the fitness of experimental evolutions). This was despite the fact that no selection pressure was dictating that increasingly fit solutions (with respect to evading predators) were selected in control evolutions. While the selection of genotypes in control evolutions was randomised (as opposed to performance-based in experimental evolutions), the bio-operators were still applied to control genotypes between generations and the resultant changes in genotypes due to the random sampling of the population was analogous to genetic drift (Rogers & Prugel-Bennett, 1999). Early investigations into protean movement tended to consider the unpredictability within movement from a general perspective and that increasing unpredictability equated to more protean and

therefore more effective evasive movement (Humphries & Driver, 1970). In chapter two, I found support for this supposition, with increasing complexity of movements generally predicting increased targeting difficulty. However, the most mathematically complex behaviours were not necessarily the most effective. Indeed, the most effective protean movements were comprised of both predictable and unpredictable elements, specifically high speed and protean turning angles (Consistent with several observed examples of protean movement, e.g. [Bilecenoğlu, 2005; Hügel & Goerlitz, 2019; Lima & Dill, 1990; Roeder, 1962]). The genetic drift of control evolutions introduced greater unpredictability into movement paths. To elaborate, in control evolutions, the narrow starting ranges of the initial generations broadened out over generational time due to the random nature of selection in control trials. While this was not directed by human performance, it nevertheless introduced greater unpredictability with respect to generated movement paths, which resulted in movement paths that were more difficult to target after 60 generations of evolutions in comparison to the movement paths from the first generation of genotypes. However, the movement paths derived from the final generation of control genotypes were still significantly easier to target than those from the final generation of experimental genotypes that were driven by human performance. Interestingly, the variance in the expressed values of turn angle for control and experimental movement paths showed no significant difference, indicating high variance in this movement characteristic was advantageous with respect to effective protean movement (Paolo Domenici, Blagburn, & Bacon, 2011; Eifler & Eifler, 2014) and was facilitated by genetic drift in control evolutions. However, the significant difference in overall fitness between control and

experimental evolutions demonstrated that the most effective protean movement in this predator-prey context is represented by a greater degree of unpredictability in the turning angle, and a lesser degree in speed and time between turns. Furthermore, variations in predator-prey context may result in the unpredictability of different aspects of movement being adaptive, for example, predictable turning as in spiralling take off flights observed in some insect species (Humphries & Driver, 1970) or unpredictable changes in speed (Edut & Eilam, 2004; Herbert-Read et al., 2013). Greater study of varying predator-prey contexts may allow further investigation into the unpredictability of individual characteristics of movement and how they may impact the effectiveness of protean movement displays.

The primary motivation for the use of the novel GA was to explore the development of protean movement strategies in several independent runs with variable starting points. This allowed me to examine both the evolutionary route which protean movements took in order to progress from less to more successful (with respect to avoiding targeting by human predators), and the variation in strategies that emerged from the human based selection pressures. The protean strategies that emerged in later generations (with the exception of the significant predictor of the timing of a turn on the fitness of protean movement strategies) were broadly consistent with the most effective paths from chapter two (i.e. high speed, protean turning angle). However, while there were minor differences in expressed values, the overall trajectory of each run of the experimental evolutions was broadly similar (see Fig.6.8). This implies that in the context of this predator prey interaction, there was a single optimum protean movement strategy which all runs converged towards. This leads me to state with some confidence that a set of principles dictating

effective protean movement in this context have been developed using the novel GA presented here. Specifically, a high movement speed and turn frequency (i.e. a low value for time between turns) with widely varying turn angles. Indeed, my previous investigations into protean movement had not demonstrated that the timing of turns was a significant predictor of protean movement efficacy. However, this study fully explored an available search space via the GA and showed that time between turns can develop to have a significant effect on fitness. This is consistent with some observations of unpredictable turn timings resulting in anti-predator benefits in certain contexts with respect to evading predators (e.g. Combes, Rundle, Iwasaki, & Crall, 2012; Driver & Humphries, 1988; Yager, May, & Fenton, 1990). While I am cautious with respect to the generalisability of this finding due to the confounds that can affect protean movement (such as number of conspecifics present, composition of group protean movement etc. [as have been explored in chapters four and five respectively]). I nevertheless suggest that the protean strategies that have emerged via the novel GA presented here are broadly representative of an optimal protean strategy for a common predator-prey interaction (i.e. a prey item detecting a predator in close proximity and attempting escape via protean movement).

In this study, real world effects on flight performance were not considered, thereby limiting the generalisability of the findings here. The study was aimed at replicating behavioural evolution, which is capable of rapid evolution at the population level (Beauchamp, 2004; Magurran et al., 1992; Massaro et al., 2008). However, regarding protean movement, over a longer timescale other heritable components would become significant factors. For example, morphological adaptations that may allow enhanced locomotory performance, plus the and

neurological architecture that may allow a wider repertoire of protean movement responses. Furthermore, the energetic and/or cognitive costs of engaging and maintaining behaviours at the extremes of an animal's abilities (including the act of behaving unpredictably) could be considerable and relevant to the evolution of effective protean movement (Cooper & Frederick, 2007; Paolo Domenici et al., 2008; French, 2010). Finally, the constraints to animal locomotion introduced by physical forces such as air resistance (Bennet-Clark & Alder, 1979), inertia (Wilson et al., 2013) and gravity (Yager et al., 1990) were not considered. In this study, the primary limitations to the development of protean movement were the amount by which genotypes were capable of change between generations and the overall upper and lower limits of the search space for each of the three movement characteristics. My rationale for the limited inclusion of constraints in the GA was that this study aimed to fundamentally examine the emergence and nature of effective protean movement in response to predatory selection pressure, with particular focus going to the relative importance of each component of movement whilst also constraining performance based on the real world capabilities of prey animals. With what I believe to be the fundaments of protean behavioural evolution established here, future research may include greater real world constraints to refine the nature of protean behavioural emergence and exhibition at a population level.

The experiment was set up to allow a full exploration of the defined search space for the three characteristics of movement. All values started in the middle of the search space where possible to allow for the development of a wide variety of behaviour (the exception being turn angle which began in lowest 5% of values). The inclusion of multiple experimental runs, with incremental changes based on human

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assessed fitness, allowed for a variety of protean strategies to potentially emerge (e.g. darting 'start-stop' movement patterns [Edut & Eilam, 2004]). It was perhaps somewhat surprising that only a generalised strategy similar to the most successful protean movement strategies observed in earlier chapters emerged. This suggests that within the parameters of this study, this strategy was substantially more fit than alternate protean strategies recorded in nature, despite the opportunity for alternatives to emerge as dominant strategies. It is plausible that alternate protean strategies would be effective in different predator-prey contexts. For example, if the predator was pursuing the prey and/ or if the predator was 'striking' at the prey as opposed to targeting only. Further changes to the context of the interaction (e.g. environmental conditions such as availability of visual obstructions [cover/ refuge]) as well as incorporating greater realism into simulations (see above) may well facilitate the emergence of alternate protean strategies and elucidate the requisite context for success of these strategies.

In conclusion, the novel Human Performance-based Genetic Algorithm which was implemented here and used to explore protean movement development has led to several intriguing findings regarding the phenomena. Firstly, emergent protean strategies conform to certain principles of protean movement previously explored while also establishing a significant effect of turn frequency which had previously resulted in non-significant effects with regards to predicting targeting difficulty. Furthermore, I have discussed a general evolutionary trend of protean movement within this context, which all independent runs of protean behavioural genotypes tended towards. The HPBGA developed and implemented here may also provide an

interesting avenue for further research into protean movement in varying contexts of predator-prey interaction.

7. General Discussion

There is a wide variety of indirect evidence in support of the anti-predator benefits of protean movement (see Table 1.1 for more details). Various authors frequently observed the erratic movements of prey animals and suggested the anti-predator benefit of the protean movements (often these studies were not investigating protean movement directly) (e.g. Paolo Domenici et al., 2011). Fewer studies have displayed direct of evidence of erratic protean movements resulting in predator evasion (e.g. Combes et al., 2012) and fewer still have directly quantified how the characteristics of protean movements relate directly to the ability of predators to target or capture prey animals (Jones et al., 2011; Sandhu et al., 2020; Tsutsui et al., 2019). Furthermore, the manner in which stimuli were presented in the aforementioned examples (i.e. vertical or horizontal movements projected on a flat surface with limited lateral range), while offering a high degree of experimental control, was less able to represent the movement qualities of a many prey species (particularly swimming or flying prey items). To elaborate, the most common behavioural response of prey is to flee *away* from predators (Krause & Ruxton, 2002), which cannot be replicated on a two-dimensional screen (as in Jones et al., 2011). The use of VR and three-dimensional representations of animal movements has allowed the representation of prey animals that are commonly associated with protean movement (i.e. swimming or flying animals [e.g. Ghose, Triblehorn, Bohn, Yager, & Moss, 2009; Herbert-Read et al., 2015; Yager et al., 1990]) from the first person perspective of a predator. Moreover, the rules given of representative prey

items in earlier studies of protean movement were relatively simple (e.g. moving randomly within a given angle and/or at a constant speed). These studies therefore did not explore some of the more intriguing observations that have been made regarding protean anti-predator movement. Specifically, the movement of real animals is dynamic and can show great variation in intra-individual and inter-individual expression (Humphries & Driver, 1970; Shaw, 2020). By introducing unpredictability into the rules of digital prey movement (i.e. speed, turn angle, time between turns), the individual and interactive effects of movement characteristics on the effectiveness of protean movement can be investigated. In this thesis I have explored the taxonomically widespread, but previously little studied phenomenon of protean movement. I have elucidated the mechanisms that allow protean behaviour to be an effective anti-predatory response via the use of VR to allow human 'predators' to attack and chase virtual prey in three-dimensions, thereby providing a deeper insight into the dynamics of common predator-prey interactions. The following are brief summaries of the key findings from each data chapter of this thesis (see Table 7.1 for overview of similarities and differences between key findings of each data chapter):

- In chapter two, I conducted an initial study into how the characteristics of a digital prey objects movement affected the targeting difficulty for human predators. I provided strong experimental support for the widely held assumption that protean strategies can reduce chances of predation. I also determined how the individual behavioural rules that make up prey movement can interact to affect the overall efficacy of protean behaviour. Specifically, I found that increasing path complexity (entropy) represented a

general predictor of increased targeting difficulty, but the individual characteristics made more robust predictors (combinations of high speed and protean variation in turning angle making the most effective paths at evading targeting). This chapter also demonstrated the practicality of VR in the study of an adaptive behaviour.

- In chapter three, I examined protean movement in a real animal model (the painted lady butterfly) in the context of passive protean movement (i.e. movement patterns that were not directly in response to a predatory threat). Digitised butterfly movements were viewed in VR by human predators. This revealed that the most effective flight characteristics consisted of low turning angles and high speeds. I also included an explanation for the general pattern of protean insurance movements and explored reasons for the occurrence of this strategy in nature.

- In chapter four, I incorporated the dynamics of prey groupings on protean movement efficacy. I investigated the interaction between the confusion effect and protean movement complexity. Specifically, whether increasing group size (which should result in an increased confusion effect) interacted with increasingly complex (i.e. 'more protean') prey movement to result in greater targeting difficulty. I used two variant approaches in the study of this question; a controlled experiment and a downloadable game utilising a citizen science methodology. Contrary to my predictions, I found no interaction between increasing group size and increasing complexity with respect to participant performance.

- In chapter five, I examined how conformity and oddity of protean movements interacted with the ability of predators to capture prey items. I found that prey items that were moving 'oddly' with respect to the rest of their grouping were preferentially and more accurately targeted than individuals that conformed with the majority in terms of the movement behaviour.

- In chapter six, I developed and implemented a novel genetic algorithm (GA) where prey movement behaviours were modified based on the ability of human participants to target them. The aim of this chapter was to explore the development of protean movement. Specifically, I investigated the relative importance of individual flight characteristics in protean movement development. I also investigated the variation and interaction of movement values that contributed to protean movement efficacy. I found that effective protean movement strategies followed a broadly similar trend and consisted of high speeds, high turn frequencies (i.e. low time between turns) and wide ranges of turning angles. I also found that similar protean strategies emerged despite some variation in the origin of the protean movement rules, suggesting a general model for effective protean movement in the predator prey context tested.

Table 7.1 Overview of the similarities and differences between the chapters in terms of their key findings of key findings of each data chapter.

Data Chapter	Key Findings
2	Entropy a significant predictor of targeting accuracy
2	Specific movement rules differed their impact on targeting accuracy
2	Highly variable turn angle and high speed predicted poorest targeting accuracy
3	Data from real animal movements provided evidence that the passive movements of butterflies could be considered a form of protean insurance-based movement
3	Entropy a significant predictor of targeting accuracy in real animal data
3	With respect to entire flight paths, increasing speed significantly predicted poorer targeting accuracy for human participants
3	With respect to the most effective movement sequences at evading targeting on a frame by frame basis, increasing speed and lower turn angles significantly predicted poorer targeting performance
4	No evidence of an interaction between group size and entropy of uncoordinated protean movements
5	In virtual prey groupings, individuals displaying 'odd' protean movement patterns were targeted preferentially, and with greater accuracy, than other conformist protean members of their group
5	No significant difference in entropy of targeted odd and targeted conformist prey items
6	Effective protean movements evolved toward increased entropy
6	Highly variable turn angle and high speed predicted poorest targeting accuracy
6	High turn frequency predicted poor targeting accuracy
6	Results indicative of a general evolutionary trend within this predator-prey context, which all independent runs of protean behavioural genotypes tended towards

The study of protean movement represents an effort to tease apart predator prey interactions on a relatively fine spatiotemporal scale. In this thesis I have investigated the holistic interaction between the characteristics of an individual's flight and the resultant effects on difficulty of capture with respect to predators. Additionally, I have explored protean behaviour in multiple contexts, including individual animals fleeing upon detection of a predatory attack (the most common

behavioural response of prey [Krause & Ruxton, 2002]), the passive protean movements that may increase the chances of evading an undetected predatory attack (Humphries & Driver, 1970) and the effect of established phenomena resulting from groupings of individuals have on protean behaviour. I will now discuss the preceding points in the context of the chapters presented in this thesis and published literature on the subject.

7.1 Movement Characteristics and Difficulty of Capture

Recent advances in behavioural ecology have led to the axiom that variation in the individual behavioural responses of individuals to a stimulus are adaptive, for example the bold-shy personality axis present in many systems (Biro & Post, 2008; Dingemanse & Wolf, 2010) as opposed to simply 'noise' surrounding a single optimum response (Dall, Houston, & McNamara, 2004). Predator prey interactions are often considered at a population level in terms of their effects on shaping community structure through its effects on predator–prey population dynamics and species diversity (Hanski, Henttonen, Korpimaki, Oksanen, & Turchin, 2001; Paine, 1966). Alternatively, the fine scale biomechanics of the physical interaction may be studied in great detail (Dudley, 1990; Schmitz, 2017). Less frequently examined are the more intermediate spatiotemporal scales that may represent (for example) a stalking predator preparing ambush a prey item. In such situations, the unpredictability that can be displayed by the individual can make a substantial difference to the survivability of the individual. Engaging in protean movement can increase the chances of evasion for prey items as the rapid sequences of complex, unsteady manoeuvres that often represent protean movement can represent

substantial challenges for predators (Combes et al., 2012; Eifler & Eifler, 2014; Major & Dill, 1978; Roeder, 1962). While predators are more likely to outpace their prey (Hirt et al., 2017) prey items may have a greater degree of agency in the interaction as they may take steps to reduce their chances of capture (i.e. engage in protean movement), while a predator must react to this behaviour (e.g. Howland, 1974; Moore & Biewener, 2015).

The advantages conferred to an individual by unpredictability are not limited to protean movement. Chance (1957) observed "audiogenic seizures" in laboratory rats. When lab technicians accidentally jangled their keys, some lab rats went into convulsions. These convulsions did not occur when the rats are provided with refugia. Chance (1957) concluded that the convulsions were facultative defensive behaviours which would make it much more difficult for a predator to catch and hold the convulsing animal in the absence of an immediate shelter. Additionally, when threatened, octopuses, cuttlefish, and sea pansies use "colour convulsions" across the fast-response chromatophores on their skin, quickly going through different colour patterns to defeat the search images (perceptual expectations) used by their predators (Driver & Humphries, 1988). Unpredictability may also provide adaptive benefits resultant from intra-species social interactions. For example, play fighting, which has been frequently reported in mammals, birds and other taxa. Pellis & Pellis (2017) suggest that the somewhat unpredictable nature of the actions of individuals involved in play fights provide learning opportunities to better adapt to future unpredictable situations. Finally, the more complicated social systems of primates demonstrate several instances of individuals benefiting from their own unpredictability. For example, unpredictable promiscuity. The outcome of sperm

competition is fairly unpredictable (Miller, 2009). Females can exploit this fact by mating promiscuously with several males during ovulation. This introduces uncertainty regarding paternity and reduces the chances of infanticide by adult males as the resultant offspring may be their own (Small, 1993). The preceding examples demonstrate that individual unpredictability may confer a wide variety of benefits in addition to protean movement.

In terms of the specific components of flight, increased path complexity has been purported to reduce the ability of predators to accurately target prey (Herbert-Read et al., 2017; Schaerf et al., 2017). This previously assumed relationship has been empirically supported several times in this thesis. Crucially however, while a good general predictor of the effectiveness of protean movements, the individual characteristics of movement represented more robust predictors of protean movement effectiveness. Increasing complexity does not necessarily result in increased protean movement effectiveness (Combes et al., 2012; Richardson et al., 2018). Indeed, the most frequently observed combination of flight characteristics that resulted in effective protean movements consisted of unpredictable turn angles and rate of turns, but a high (i.e. predictable) speed. Most notably this combination of flight characteristics consistently emerged as a generalised protean strategy when under sustained and consistent predation pressure. This consistent finding in this thesis indicates that the relationship between the unpredictability of flight characteristics and effective protean movement is somewhat nuanced and the most effective protean movement is unpredictable 'where it counts' (i.e. in turning and timing of turns).

However, while this thesis has examined the interactions of flight characteristics and protean movement efficacy in great detail, it has been demonstrated that the context of the interaction has arguably the largest influence on what makes protean movement effective. Protean movement can offer benefits to prey items whether they are aware of predators or not, but the values that result in the greatest benefit are dependent on the context.

7.2 Predator – Prey Context and Protean Movement

A wide array of factors can influence the behaviour engaged by prey animals in response to predators. More recent models of prey escape decisions have tended to take an economic perspective and consider the fitness costs and benefits of escape, thereby making qualitative predictions about aspects of escape behaviour (Cooper & Blumstein, 2015; Cooper & Frederick, 2007; P. Domenici et al., 2011; Eifler & Eifler, 2014). The decision to engage in anti-predator behaviour (including protean behaviour, seeking refuge, freezing etc.) often varies in response to the perceived level of threat posed. For example, fleeing from a distant predator may not be assessed as economical with respect to losing opportunities to engage in other fitness increasing activities such as feeding and engaging in social activities including courtship, mating and territorial defence (Cooper & Blumstein, 2015). This has been demonstrated by Herbert-read et al. (2015), who showed that Pacific blue-eyes (*Pseudomugil signifer*) responded to a threatening stimulus by expressing protean movement if the stimulus was in close proximity to the individual, but not when the threat was further away. This demonstrates the effect that the context of the predator prey interaction can have on protean movement expression. To that end,

this thesis explored different predator prey contexts and the effects that these had on the expression and efficacy of protean movement. These contexts included protean movements representative of escape responses (i.e. escaping away from the predatory threat as is the most common reaction from prey animals [Krause & Ruxton, 2002]) in chapters two and six. Additionally, due to the implementation of the genetic algorithm, prey items in chapter six were responding indirectly on a genotypic level to selection pressure, thereby altering expressed behaviour. Chapter three studied real animal movement patterns and their passive protean movement, or 'protean insurance' (Humphries & Driver, 1970) when the targets (butterflies) were more distant from the predator, while chapters four and five involved multiple prey items in groupings. What was not implemented or studied in this thesis was active evasion by prey items in direct response to the gaze or strikes of a predator (see below: Research limitations).

While the evidence from chapter three suggests that high turn angles are less effective at avoiding targeting when at a moderate distance, it has been demonstrated that the occurrence of a turn (regardless of its angle) can be effective when a predator has intercepted a prey item and is within striking range (Combes et al., 2012). The differences in the findings highlights the effect that the contextual difference can have on the flight characteristics required for effective protean movement. Modern views of predator prey interactions on a community level consider the variations in predator and prey morphology, behaviour, and physiology that can affect the context of interactions. Examples include predator and prey body size, predator and prey personality, predator hunting mode, prey mobility and prey physiological stress (Schmitz, 2017). These characteristics are referred to as

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'functional traits'. Variations in functional traits and the resultant effect on the predator prey context influence the overall effectiveness of any protean movement displayed. By virtually representing prey movement, the functional traits of both predators and prey can be manipulated to investigate the effects on protean movement performance. Specific suggestions are discussed in more detail in the following section.

In addition to the functional traits of individual predators or prey items, the presence or absence of conspecifics represents a social context that must also be considered when investigating protean movements. A great many prey items are gregarious in nature and therefore spend all or significant parts of their life history in groups of conspecifics or heterospecifics (Mathis & Chivers, 2003; Miller, 1922). There are many costs and benefits associated with group living (Lehtonen & Jaatinen, 2016), however, the interaction between these factors and protean anti-predator movement are mostly unexplored. Investigations into group effects and their interaction with protean anti-predator movement therefore highlight another layer of complexity in this discipline. Characterizing the effects of the predator prey context on protean movement efficacy offers a way to better understand the complex relationships that are inherent to predator–prey interactions.

7.3   Research Limitations

In all chapters detailed here, the gaze of human participants was included as a metric of targeting ability and therefore the vulnerability of each prey item to capture. While this is consistent with the ability of a predator to capture an a prey item (Olberg et al., 2000), other methods, such as eye tracking may offer increased precision in terms

of quantifying the ability to target an item. This may in turn more precisely identify effective protean strategies. To elaborate, 'smooth pursuit movements' allow the eyes to closely follow a moving object (Robinson, 1965) while 'saccadic' eye movements occur when the eyes make larger adjustments (i.e. an object traverses a visual angle greater than ~0.17π radians/s [Gegenfurtner, 2016]). The combination of eye tracking and head orientation could more accurately determine the qualities of protean movement that cause rapid eye movements or overall accuracy of smooth pursuit movements. Furthermore, eye tracking devices that are integrated with popular VR systems are now affordable, commercially available and have already seen use in academic studies (Pettersson et al., 2018). Eye tracking could be integrated into existing VR simulations to more closely examine how protean movement strategies affect the ability of human participants in targeting them. With only head movement-based targeting, the data utilised in analyses may lack the granularity to precisely determine which components of protean movement result in reduced targeting accuracy.

The use of digital animals and VR provide many advantages, including the ease of generating large sample sizes and the circumvention of ethical considerations. All data chapters in this thesis feature digital animals that were constrained by the limits of real animal performance data where possible. However, with the exception of chapter three, the movement paths that were drawn using this data were not subject to physical constraints. For example, in general for flying animals, as body mass increases, so too does speed at the cost of reduced manoeuvrability (Ellington, 1991). Furthermore, the medium through which animals move greatly influences the qualities of movement that can be expressed. For

example, the spinning loops and powered dives reported in aerial insects (Ghose et al., 2009; Roeder, 1962; Yager et al., 1990) are unlikely to represent a practical protean movement strategy in aquatic environments. Furthermore, for increasingly massive animals to engage in protean movement they must account for physical principles that impact their ability to move with the agility of smaller animals (i.e. square cube law [Meyer-Vernet & Rospars, 2015]). I did not represent these physical constraints here and as such, the studies detailed in this thesis are most analogous to aerial prey items thereby limiting the generalisability to protean movements in aquatic or terrestrial environments. In chapter three, which utilised real animals data, butterflies were chosen as they were relatively slow flying and highly tractable. Their low mass meant that they were less affected by inertia with respect to their ability to turn tightly without sacrificing speed. This meant that comparisons to simulations here, with no physical constraints were more applicable. Despite this however, the butterfly data still showed a significant trade-off between speed and turning angle, with narrower turning angles at higher speeds. Furthermore, the effect of gravity allowed assisted dives and also resulted in slow ascents. As this thesis set to establish the principles of effective protean movement, I chose to forgo certain physical constraints that could confound conclusions. While I am confident that the fundamental principles of protean movement established in the preceding data chapters are sound and apply in general to a wide variety of predator-prey situations, it is clear that the physical constraints that operate in real world situations affect the expression of effective protean movement (see Future Avenues of Research).

In all studies, the movement of prey items did not respond directly to being targeted by predators. It has been demonstrated that when a prey item is aware of

a predators position, engaging in a well-timed unpredictable direction change can help prey animals evade capture. The most notable example of this principle is the 'turning gambit'. In this scenario, prey items that are outpaced by a pursuing predator are often capable of superior manoeuvrability (typically due to being less massive and therefore possessing less inertia at higher speeds allowing sharper turning, in addition to being the 'actor' as opposed to the predatory 'reactor' [Hirt et al., 2017]). The execution of an unpredictable change in direction by the prey item when the predator is in very close proximity may result in an increased distance between predator and prey allowing more opportunities for the prey to escape (Howland, 1974). The turning gambit is only successful when the prey is cognisant of the predators relative position to itself. As the research in this thesis did not replicate active evasion, this limits to generalisability of the interpretations that can be made. It is worth noting however, that turning gambits are primarily relevant for pursuit/ evasion contexts and the predator prey contexts primarily studied here were representative of a stalking/ ambush predator where the prey item had not detected the predator.

7.4 Future Avenues of Research

Direct study into protean movement has been relatively infrequent and sparse (Jones et al., 2011; Richardson et al., 2018; Sandhu et al., 2020; Tsutsui et al., 2019). This thesis has closely examined the factors that control the effectiveness of protean movement in several scenarios. However, regarding the study of protean movement, there are a number of relevant areas that warrant further exploration. This includes the interaction between prey colouration and protean movement efficacy, the ability

of predators to learn protean movement strategies at an individual and population level, how variations in the context of the predator-prey interaction (particularly in terms of the effectiveness of protean movements when confronted with different predator hunting tactics) and the implementation of further physical constraints more representative of real world situations.

The inclusion of physical laws in simulations such as gravity, air resistance, inertia etc. would facilitate the study of protean movement at a greater depth. It would allow the specific examination of predator-prey systems. Simulations of both predators and prey animals could involve more realistic physical constraints. (e.g. Terzopoulos, Tu, & Grzeszczuk, 1994) to more accurately simulate the effects of animal size or environmental conditions (i.e. aquatic vs aerial) on the ability of predators to capture protean prey. Furthermore, the generalisability of protean movement principles established here could be tested with differing systems in differing mediums (i.e. aerial vs aquatic, small predator prey systems vs large predator prey systems). Including simulated constraints representative of real-world systems, could facilitate greater realism of predator prey interactions while retaining the advantages of the digital approach.

In addition, there are a variety of hunting tactics that are employed by predators including ambush and pursuit predation. The latter of which is often used by groups of predators (Gazda, Connor, Edgar, & Cox, 2005; Stander, 1992). Groups of pursuit predators often attempt to coordinate with conspecifics to separate prey items from their grouping (Southern & Kruuk, 1973). Protean movement efficacy could be explored with respect to sophisticated hunting tactics using variations of

the VR methodologies detailed in this thesis. For example, by allowing participants to coordinate with a 'conspecific' predator or directly capture protean prey items (i.e. giving them an ability to 'strike' etc as in the FlyCatcher citizen science game). Furthermore, protean escape paths may be relatively ineffective against predators that do not target individual prey but rather capture large numbers of prey by moving through dense swarms (e.g. whales feeding upon krill). Manipulating the area of effect of a capture attempt could more effectively replicate these predatory tactics and therefore which protean strategies (if any) would be effective.

The impact of specific forms of colouration and protean behaviour is also mostly unexplored. Cryptic colouration typically operates when an animal is stationary and is ineffective if the animal is forced to move (i.e. it is detected by a predator) (Hall et al., 2013). How might salient features of cryptic colour patterns (originally concealing the prey) affect a predator's ability to target the item, even if it is moving with supposedly effective protean movements? Furthermore, certain conspicuous colouration patterns, while not cryptic are purported to reduce the ability of predators to target the conspicuously coloured prey (thereby reducing the chances of capture by a predator). The most conspicuous example of this being 'motion dazzle', where rapidly moving bold patterns of contrasting stripes (i.e. zebra [*Equus spp.*]), seem to confuse an observer's visual processing and prevent effective targeting. This phenomenon has only recently been shown to increase the difficulty of capture (How & Zanker, 2014; Scott-Samuel et al., 2011; Stevens, Searle, Seymour, Marshall, & Ruxton, 2011). Protean movement patterns may interact with the motion dazzle camouflage to increase the difficulty of targeting the item (in comparison to a target without this pattern).

Indeed, while chapters four and five investigated group based effects and protean movement, the work presented in this thesis has primarily explored protean movement in isolation of other anti-predator behavioural strategies. In real world predator-prey interactions, a prey animal will have access to a wide range of behavioural responses to a predatory threat. These include deimatic displays (Merilaita et al., 2011), pursuit-deterrent signals (Stankowich & Coss, 2007) or creating distractions (i.e. cephalopod spp. ejecting ink clouds) (Derby, 2007). While certain anti-predator behavioural responses are fundamentally different in their nature (i.e. crypsis is typically only effective when the prey item is static), the antipredator behaviours listed above primarily occur during locomotion. Furthermore, in nature, a range of responses may be expressed simultaneously during a predator-prey encounter, whether during an ambush or over a longer pursuit. To elaborate, protean movement may, or may not be included in combination with certain anti-predator behaviours. Through the use of VR and human participants granting a fully-controlled environment, future research could perhaps quantify the relative merits of a wide range of dynamic anti-predator behavioural responses and their relative effectiveness with respect to (or in combination with) protean movement. A quantification of the proportionate effectiveness of common behavioural responses to a predatory threat could further advance the current understanding of adaptive prey behaviour and is well suited to the digital approach.

7.5 Conclusions

In this project I have examined the understudied phenomenon of protean movement in a variety of contexts, utilising several novel methodologies. The overall aim of this project was to evaluate the mechanisms by which the unpredictable protean movements of prey animals form an effective anti-predator behaviour. The degree of control afforded by virtual prey populations has allowed the in depth exploration of the complexities of protean anti-predator movement in a wide range of predator-prey contexts. Over the course of this thesis, I have contributed to the understanding of protean movement in a number of ways. Firstly, I demonstrated that effective protean movement can be characterised by the incorporation of unpredictability into some (but not necessarily all) components of movement. For example, when replicating an active evasion from a predator, a protean prey item is unpredictable in turn angle and turn rate, while displaying consistently high speed. In this case, protean movement is characterised, not by overall randomness of flight characteristics, but by the application of unpredictability in specific aspects of movement. However, I have also shown that the context of the predator-prey interaction has a great effect on what constitutes an effective protean movement. For example, in an alternative predator-prey context, such as flight of butterflies in the absence of a predatory threat, the characteristics of movement corresponding to effective protean movement were different, with higher speeds and narrower turning angles (often indicative of dives) representing the most effective protean movement. Additionally, in looking at the movements of butterflies, I have provided empirical support for the previously held supposition that the passive movements of these animals can constitute protean insurance, reducing their chances of capture

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without the detection of a predatory threat. Furthermore, when looking at the interaction between protean movement and groupings of animals, I reported several interesting findings. Firstly, when investigating the interaction between group size and uncoordinated protean movement via a locally controlled experiment and a citizen science game, I found no discernible interaction between increasing group size and increasing protean movement complexity with respect to the difficulty of capturing prey items. This implies that the efficacy of protean movement from uncoordinated individuals within a group is not enhanced by the confusion effect resultant from the presence of more individuals. Furthermore, I have demonstrated that anomalous protean movement of an individual relative to other group members can induce a behavioural oddity effect resulting in the preferential and more accurate targeting of the odd individual. This suggests that while an individual's protean movement may be effective in isolation, it may be conspicuous in a group. This therefore provides an explanation for the commonly observed attenuation of individuality when individuals join groups on conspecifics. Finally, using a novel genetic algorithm, I demonstrated that when subjected to sustained predation pressure, protean movement strategies at a population level all developed toward a consistent optimal strategy. While the predator-prey context utilised in this study represents one example of many potential predator-prey contexts, it nonetheless demonstrates how adaptive protean movement may develop in response to common predation pressures. Furthermore, the GA described and implemented here represents a suitable framework to investigate further predator-prey contexts with respect to the effective protean movement strategies that may emerge. The primary conclusions of this thesis have therefore facilitated a deeper understanding of a near

ubiquitous component of predator-prey interactions that has until recently been the subject of little empirical study. These findings are directly applicable to predator-prey dynamics within a broad range of taxa.

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9. Appendix A – Model outputs

This appendix contains the minimum adequate model outputs of generalised linear mixed-effect models (glmm) in R version 3.3.2, using the lmer and glmer functions (for linear mixed models and logistic regression, respectively) in the lme4 package (Bates et al., 2015). Additionally, output tables include model estimates, standard error, degrees of freedom, t-values and p-values. Significance stars are also included: * p < 0.05, ** p < 0.01, *** p < 0.001. Data is presented to 2 s.f.

9.1 Chapter Two

9.1.1 Path complexity

	Value	Std.Error	DF	t-value	p-value	Significance
(Intercept)	-0.75	0.03	1038	-23.16	0.00	***
entropy	0.12	0.01	1038	9.57	0.00	***
trial	0.00	0.00	1038	-0.73	0.47	

	Value	Std.Error	DF	t-value	p-value	Significance
(Intercept)	0.079511	0.007933	1036	10.02233	0	***
protean.f1	0.254361	0.00731	1036	34.79593	0	***
protean.f2	0.295961	0.008653	1036	34.20439	0	***
protean.f3	0.32699	0.016987	1036	19.24929	0	***
trial	-0.00058	0.000396	1036	-1.47489	0.1405	

	Value	Std.Error	DF	t-value	p-value	Significance
(Intercept)	-0.57184	0.024611	1036	-23.2353	0	***
protean.f1	0.067949	0.019394	1036	3.503602	0.0005	***
protean.f2	0.095461	0.022956	1036	4.158403	0	***
protean.f3	0.143559	0.045068	1036	3.185388	0.0015	***
trial	-0.00092	0.001052	1036	-0.87669	0.3809	

	Value	Std.Error	DF	t-value	p-value	Significance
(Intercept)	0.298839	0.007169	1036	41.68221	0	***
protean.f.L	0.228654	0.011538	1036	19.81702	0	***
protean.f.Q	-0.11167	0.009388	1036	-11.8942	0	***
protean.f.C	0.045211	0.006581	1036	6.86944	0	***
trial	-0.00058	0.000396	1036	-1.47489	0.1405	

	Value	Std.Error	DF	t-value	p-value	Significance
(Intercept)	-0.4951	0.022902	1036	-21.6184	0	***
protean.f.L	0.102454	0.030612	1036	3.346891	0.0021	***
protean.f.Q	-0.00993	0.024907	1036	-0.3985	0.6903	***
protean.f.C	0.013645	0.017461	1036	0.781462	0.4347	***
trial	-0.00092	0.001052	1036	-0.87669	0.3809	

9.1.2 Movement rules

	Value	Std.Error	DF	t-value	p-value	Significance
(Intercept)	-0.37	0.02	1029	-16.47	0.00	***
anglerandom	0.13	0.02	1029	6.64	0.00	***
anglewide	0.08	0.02	1029	3.98	0.00	***
speedlow	-0.54	0.02	1029	-28.02	0.00	***
speedrandom	-0.15	0.02	1029	-7.99	0.00	***
distancerandom	0.02	0.01	1029	1.64	0.10	
distanceshort	0.00	0.01	1029	-0.30	0.76	
trial	0.00	0.00	1029	0.62	0.54	
anglerandom:speedlow	0.00	0.03	1029	0.00	1.00	
anglewide:speedlow	0.05	0.03	1029	1.83	0.07	
anglerandom:speedrandom	-0.10	0.03	1029	-3.53	0.00	***
anglewide:speedrandom	0.00	0.03	1029	-0.08	0.93	

9.2 Chapter Three

9.2.1 Does butterfly flight path entropy predict human performance?

	Estimate	Std.Error	DF	t-value	p-value	Significance
(Intercept)	-1.75	0.17	38.26	-10.08	0.00	***
entropy	0.14	0.04	38.00	3.27	0.00	**
trial.order	0.00	0.00	1521.00	8.95	0.00	***

9.2.2 Do overall butterfly flight characteristics predict human performance?

	Estimate	Std.Error	DF	t-value	p-value	Significance
(Intercept)	-1.11	0.03	45.40	-32.59	0.00	***
speedLow	-0.13	0.04	38.00	-3.12	0.00	**
trial.order	0.00	0.00	1521.00	8.95	0.00	***

9.2.3 What characterises effective butterfly movements on a finer temporal scale?

This analysis was a logistic regression

	Estimate	Std.Error	z-value	p-value	Significance
(Intercept)	-9.0373	2.1094	-4.284	1.83E-05	***
log10(speed)	1.8125	0.265	6.839	7.98E-12	***
log10(turn.angle)	-0.4466	0.1373	-3.251	0.00115	**

9.3 Chapter Four

9.3.1 Experiment 1 (Local data collection)

9.3.1.1 Group size and protean movement efficacy

	Estimate	Std.Error	DF	t-value	p-value	Significance
(Intercept)	8.03	0.07	5388	122.83	0.00	***
densityModerate	0.56	0.05	1035	-10.77	0.00	***
densityHigh	0.50	0.05	1035	-9.64	0.00	**
trial.order	0.00	0.00	1035	0.42	0.68	

9.3.2 Experiment 2 (Citizen science game)

9.3.2.1 Group size and protean movement efficacy

	Estimate	Std.Error	DF	t-value	p-value	Significance
(Intercept)	0.41	0.05	97.71	8.92	0.00	***
NumFlies	-0.03	0.00	137.99	-5.80	0.00	***
TrialOrder	0.01	0.00	142.00	2.84	0.01	**

9.4 Chapter Five

9.4.1 Targeting accuracy

	Estimate	Std.Error	DF	t-value	p-value	Significance
(Intercept)	-3.49	0.01	3.76	-577.27	0.00	***
conformist	0.25	0.00	5998.00	65.72	0.00	***
control	0.19	0.01	1.42	23.57	0.01	**
trial.order	0.00	0.00	4408.00	4.58	0.00	***
participant	0.00	0.00	5998.00	-41.56	0.34	

9.4.2 Proportion of time targeting

	Estimate	Std.Error	DF	t-value	p-value	Significance
(Intercept)	0.15	0.02	1995	9.71	0.00	***
conformist	-0.01	0.01	1995	-0.83	0.40	
control	0.04	0.01	1995	3.20	0.00	**
trial.order	0.00	0.00	1995	-1.23	0.22	
participant	0.00	0.00	1995	-2.71	0.71	

9.4.3 Targeted item complexity and prey type

	Estimate	Std.Error	DF	t-value	p-value	Significance
(Intercept)	3.70	0.02	495	153.29	<2e-16	***
prey.contextControl	0.00	0.01	11600	-0.32	0.75	
prey.contextOdd	0.00	0.01	11600	0.31	0.76	
trial.order	0.00	0.00	11930	0.09	0.93	
participant	0.00	0.00	398	-0.21	0.83	

9.5 Chapter Six

9.5.1 Targeting accuracy (fitness)

	Estimate	Std.Error	DF	t-value	p-value	Significance
(Intercept)	0.37	0.05	334.80	7.42	0.00	***
generation	0.01	0.00	462.50	7.58	0.00	***

9.5.2   *Entropy*

	Estimate	Std.Error	DF	t-value	p-value	Significance
(Intercept)	0.73	0.07	5.07	10.43	0.00	***
generation	0.01	0.00	71930.00	59.28	0.00	***
typeexp	0.06	0.01	71930.00	8.74	0.00	***
generation:typeexp	0.02	0.00	71930.00	87.55	0.00	***

9.5.3   *Flight characteristics*

	Estimate	Std.Error	DF	t-value	p-value	Significance
(Intercept)	2.43	0.16	8.24	14.86	0.00	***
gen.and.speed60_ctrl	-0.24	0.03	4672.07	-9.02	0.00	***
gen.and.speed60_exp	1.94	0.03	4671.78	73.37	0.00	***

	Estimate	Std.Error	DF	t-value	p-value	Significance
(Intercept)	1.28	0.07	6.39	18.63	0.00	***
gen.and.time60_exp	-0.95	0.01	7649.64	-71.36	0.00	***
gen.and.time60_ctrl	-0.51	0.02	7647.52	-31.97	0.00	***

	Estimate	Std.Error	DF	t-value	p-value	Significance
(Intercept)	5.60	3.09	6.75	1.81	0.12	
gen.and.angle60_exp	43.82	0.80	7643.09	55.12	0.00	***
gen.and.angle60_ctrl	33.42	0.96	7638.71	34.97	0.00	***

10. Appendix B – Additional research output

Additional research output from duration of this research project:

O'Hare, L., Sharp, A., Dickinson, P., **Richardson, G**., & Shearer, J. (2018). Investigating head movements induced by 'Riloid' patterns in migraine and control groups using a virtual reality display. Multisensory Research, 31(8), 753–777.

Abstract

Certain striped patterns can induce illusory motion, such as those used in op-art. The visual system and the vestibular system work together closely, and so it is possible that illusory motion from a visual stimulus can result in uncertainty in the vestibular system. This increased uncertainty may be measurable in terms of the magnitude of head movements. Head movements were measured using a head-mounted visual display. Results showed that stimuli associated with illusory motion also seem to induce greater head movements when compared to similar stimuli. Individuals with migraine are more susceptible to visual discomfort, and this includes illusory motion from striped stimuli. However, there was no evidence of increased effect of illusory motion on those with migraine compared to those without, suggesting that while motion illusions may affect discomfort judgements, this is not limited to only those with migraine.

Hicks, K., Gerling, K., **Richardson, G.**, Pike, T., Burman, O., & Dickinson, P. (2019).

Understanding the effects of gamification and juiciness on players. In 2019

IEEE Conference on Games (CoG) (Vol. 2019-Augus, pp. 1–8). IEEE.

<u>Abstract</u>

Gamification is widely applied to increase user engagement and motivation, but empirical studies on effectiveness are inconclusive, and often limited to the integration of tangible elements such as leaderboards or badges. In this paper, we report findings from a study with 36 participants that uses the lens of Self-Determination Theory to compare traditional gamification elements, and the concept of juiciness (the provision of abundant audio-visual feedback) in the VR simulation "Predator!". Results show that gamification and juiciness improve user experience, but that only juiciness fulfils all basic psychological needs that facilitate intrinsic motivation when applied in non- gaming settings. User preferences favour the combination of both approaches, however, neither improved performance, and there is evidence of juicy elements influencing user behaviour. We discuss implications of these findings for the integration of gamification, reflect on the role of both approaches in the context of feedback, and outline challenges and opportunities for further research.