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RESEARCH ARTICLE

Escape path complexity and its context dependency in Pacific blue-eyes (*Pseudomugil signifer*)

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ABSTRACT

The escape paths prey animals take following a predatory attack appear to be highly unpredictable – a property that has been described as 'protean behaviour'. Here, we present a method of quantifying the escape paths of individual animals using a path complexity approach. When individual fish (*Pseudomugil signifer*) were attacked, we found that a fish's movement path rapidly increased in complexity following the attack. This path complexity remained elevated (indicating a more unpredictable path) for a sustained period (at least 10 s) after the attack. The complexity of the path was context dependent: paths were more complex when attacks were made closer to the fish, suggesting that these responses are tailored to the perceived level of threat. We separated out the components of speed and turning rate changes to determine which of these components contributed to the overall increase in path complexity following an attack. We found that both speed and turning rate measures contributed similarly to an individual's path complexity in absolute terms. Overall, our work highlights the context-dependent escape responses that animals use to avoid predators, and also provides a method for quantifying the escape paths of animals.

KEY WORDS: Protean behaviour, Entropy, Escape behaviour

INTRODUCTION

Prey have evolved an array of behaviours in order to avoid or discourage predatory attacks, such as stotting (FitzGibbon and Fanshawe, 1988), thanatosis (Miyatake et al., 2004) and defensive regurgitation (Schmidt, 1990). But when an attack is inevitable or already initiated, the most common defence a prey uses is to flee, thereby attempting to maximise the instantaneous distance between itself and the threat (Weihs and Webb, 1984). These escape responses involve both non-locomotor and locomotor components (Domenici et al., 2007), and for some animals, are initiated when the apparent looming rate (the rate at which an object's angular size appears to change on an individual's retina) reaches some threshold (Santer et al., 2012; Domenici, 2002). Non-locomotor components of these behaviours include the escape latency and the reaction distance to the threat, whilst locomotor components include the turning and tangential speeds of an escape path (Domenici et al., 2007). The timings and directions of these escape responses are context dependent (Domenici, 2010; Eaton and Emberley, 1991) and rely on integrating information on the distance and direction of an approaching threat (Hemmi and Pfeil, 2010; Domenici et al., 2011). The flight initiation distances of the grasshopper *Psinidia fenestralis*, for example, changes under repeated attacks (Bateman and Fleming, 2013). Further, the initial escape direction animals take (with regards to the direction of attack) can also be highly variable (Domenici et al., 2011; Domenici and Blake, 1993; Eaton and Emberley, 1991). Cockroaches, for example, have multiple preferred directions of escape (Domenici et al., 2008). In other cases, directions of escape may be limited by the locomotory constraints on an animal's movements or obstacles (Domenici et al., 2011; Eaton and Emberley, 1991). Escape behaviour, therefore, is a classic example of how an animal can rapidly integrate information from its environment to produce an appropriate behavioural response that is constrained by the animal's biomechanics and information processing capabilities.

In fishes, there are typically three stages to an individual's escape response; (1) the preparatory stage, (2) the propulsive stage and (3) the final stage (Weihs, 1973). The first and second stages of the escape response have been studied extensively (Eaton et al., 1977; Domenici and Blake, 1997), and these stages can last less than 40 ms (Domenici and Blake, 1997). Together with the final stage of the escape response, which can involve both acceleration and deceleration responses over longer periods of time, these three stages make up the escape path of an animal. Often these escape paths appear to be highly complex, a property that has been termed 'protean' behaviour (Driver and Humphries, 1988; Humphries and Driver, 1970). The complexity of an animal's path can be attributed to them reducing the predictability of their movements in order to avoid predators intercepting them, or to increase the likelihood that a predator abandons the chase (Jones et al., 2011). To date, difficulty in quantifying these paths have made these observations largely anecdotal, making it difficult to compare this behaviour with varying conditions and contexts. Whilst instantaneous measures such as the escape direction, tangential speeds, acceleration and turning rates of an individual can all be measured separately (Walker et al., 2005), how these variables combine to increase the unpredictability of an animal's path over time remains unclear. These instantaneous measures provide key insights into predator–prey dynamics and are important in determining whether prey survive following single strikes (Webb, 1976, 1982; Fuiman, 1993; Eaton et al., 1977; Eaton and Emberley, 1991; Fuiman et al., 2006). However, considering some predators actively chase their prey (Domenici et al., 2014; Neill and Cullen, 1974), if an animal can sustain high levels of path complexity, then this is likely to be a strong determinant of its survival chances.

Simply increasing path complexity, however, may not be adaptive under all contexts. When an animal is further from the threat, it has more time to implement an escape plan that could involve seeking cover (Rahel and Stein, 1988) or freezing

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(Quinn and Cresswell, 2005). We set out to quantify how an animal integrates turning rate and speed changes in its escape path following an attack over longer periods than previously analysed. In particular, we wanted to know how unpredictable an animal's path became following an attack. We also asked whether the predictability of an escape path was context dependent, and changed as a function of the distance or direction to the threat.

MATERIALS AND METHODS

Experimental procedure

Pacific blue-eyes (*Pseudomugil signifier* Kner 1865) were caught in hand nets from Narrabeen Lagoon, New South Wales, Australia (33°43′03″ S; 151°16′17″ E), and were housed in 150 l aquaria. These fish are a facultative shoaling species found both on their own and in groups of various size (Pusey et al., 2004; Herbert-Read et al., 2010). Fish (∼2–3 cm standard length) were held for at least 2 weeks prior to experimentation. They were kept under a 12 h:12 h dark:light photoperiod and were fed flake food *ad libitum*. Fish were fed on the evening after trials had been completed. An annulus arena (760 mm external diameter, 200 mm internal diameter) was filled to a depth of 70 mm with aged and conditioned tap water. The stimulus, a 6 cm^2 piece of 2.5 mm-thick opaque black plastic fixed to the end of a white rod, 4 mm in diameter, was angled so that it could be horizontally extended 200 mm into the arena (at a height of 2–3 cm above the water's surface). A camera (Logitech Pro 9000) placed directly above the centre of the arena filmed the experiments at 15 frames s^{-1}. This temporal resolution is typically lower than that of other studies (Domenici and Batty, 1997; Marras et al., 2011), but here we analyse the escape behaviour over longer periods. The arena was lit by fluorescent lamps and was visually isolated. See Fig. S1 and Movie 1 for a setup of the experimental arena.

For each trial, we placed a single fish (n=77) into the arena and waited for 3 min to allow the fish to acclimate to the new environment and explore the arena. Each fish was only used once. Following these 3 min, the stimulus was extended into the arena. The stimulus was designed to mimic the strike of an aerial predator, and the fish exhibited a strong evasive response to it even though it did not break the water's surface (Movie 1). The stimulus was introduced when the fish were in different locations within the arena. Because of the shape and width of the stimulus and its location above the water, it is unclear how the fish would have perceived the stimulus. Therefore, we chose to study how the fish's behaviour varied with the distance or direction they were facing in relation to the threat, and not measures such as looming rates or translational velocities of the stimulus.

Films were converted from .wmv format to .avi using DirectShowSource and VirtualDub (v 1.9.2). Fish were subsequently tracked using CTrax (Branson et al., 2009). We manually corrected any errors the tracking software had made using the associated Fixerrors GUI in MATLAB, giving the raw x,y co-ordinates of a fish's position at every time step. Any fish that did not move at least 1 cm in the second before the attack was removed from analysis. This was because small tracking artefacts could artificially inflate a fish's path complexity if it was not moving. In total, four trials were removed. To ensure our context-dependent results were not due to non-reacting fish, we removed a further two trials where the fish could not have seen the stimulus when it entered the arena. Hence our total number of replicates equals 71. We calculated the distance of the fish to the nearest wall, and the angle between the fishes' heading and the vector pointing from the fish's position to the stimulus' final resting place with custom scripts in MATLAB (Fig. S2). There was a strong correlation between this angle in the frame before the stimulus entered the arena, and at the frame when the stimulus came to its final resting place (R=0.54, n=71, P<0.0001).

Path complexity

We used an information-theoretic measure of path complexity or randomness developed previously for studying changes in the movement patterns of navigating pigeons (Roberts et al., 2004). This measures the informational complexity of the intervals of the movement path. We use this in a novel sense to give a measure of how well an escaping fish's movements could be predicted by a potential predator. More complex paths cover a greater range of different speeds and turning rates, with complexity defined as the entropy of the probability distribution needed to specify all the vectors in the interval. Thus complexity gives an indication of how well a predator could infer the likely future location of the fish from its recent movements. Straight line movement can be described very simply, with a direction and a distance. Conversely, complex motion requires much more information to describe. Natural animal motion lies between these extremes (Roberts et al., 2004; Guilford et al., 2004). Defining path complexity in this information-theoretic manner gives a more fundamental measure of the unpredictability of an animal's motion than related measures such as tortuosity (Roberts et al., 2004).

The complexity of a path segment is derived by considering an embedding matrix, **M**, containing the recorded positions of the animal over a time window, t, t+1, …, t+n. For the results reported in this paper, we use a time window of 0.5 s, which we find gives the best balance between the temporal precision in fixing the complexity to the path and the degree of noise in the complexity. At 15 frames s^{-1} this gives a time window of eight time steps. The x component of the embedding matrix is specified from the x co-ordinates of the positions as below:

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

with $\mathbf{M}_y$ specified similarly from the y co-ordinates. The full embedding matrix is then the concatenation of the two:

$$\mathbf{M} = [\mathbf{M}_x \mathbf{M}_y]. \qquad (2)$$

Before calculating the complexity of the embedding matrix, we first subtract the mean for each column, to focus on variation around the mean position within the window, creating a new matrix **M′**. The complexity of the segment, H, is taken as the entropy of the distribution of the singular values, taken from a singular value decomposition of **M′**. We measure entropy in bits, which is equivalent to using base 2 for the logarithm. We proceed by performing the singular value decomposition on **M′** and calculating the entropy of the normalised eigenvalues as shown below:

$$\mathbf{M}' = \mathbf{USV}, \quad s_i = S_{ii}, \quad \hat{s}_i = s_i / \sum_{i=1}^{n} s_i, \qquad (3)$$

$$H = -\sum_{i=1}^{n} \hat{s}_i \log_2 \hat{s}_i, \qquad (4)$$

where **U** is a matrix of left singular vectors from the singular value decomposition of **M**, **V** is a matrix of right singular vectors and **S** is a diagonal matrix whose diagonal component S_{ii} is the ith eigenvalue of **M**. This measure of complexity is, strictly speaking, a property of the path segment, rather than an instantaneous value. In this study we take the complexity at time *t* to be the entropy of the path segment that ends at time *t*, as this is the first point at which the recorded position from *t* enters the calculation. Therefore, this is when we expect to begin seeing the effect of the stimulus. It is important to note that this measure of path complexity is scale, translation and rotation independent (Roberts et al., 2004), meaning that the absolute mean position, orientation and speed of the fish within the time window will not alter the complexity.

Separation of turning rate and speed complexity

To identify whether the complexity of the escape path is determined by variation in turning rate or speed, or both, we adapted the path complexity measure to isolate these components. To calculate a purely turning rate measure of complexity, we first reconstructed the escape path, retaining the direction of each movement vector but normalising the displacement per time step to a unit size. It is important to note here that the path entropy is not calculated directly from the angles, or the angles turned per second of the fish. Instead, it is calculated from the reformed ‘path’ once the speed information has been removed. However, because the frame rate is consistent, this measure could be interpreted as how much information is contained in the ‘turning rate’ of a fish. Similarly, to isolate the speed component, we reconstructed the escape path retaining the size of displacement for each movement vector but standardising all movement directions to lie along a straight line. We then applied the path complexity measure to these reconstructed paths to calculate turning rate or speed complexity, respectively.

Statistics

We used linear regression models to assess the relationship between path complexity and the variables we were interested in, including appropriate controls for additional potential sources of variable complexity. For example, to test for context dependency in proximity to the stimulus, we used a linear model specified as: complexity~distance to stimulus+distance to nearest wall+angle to the stimulus.

Control variables were included to compensate for any biases in the data dependent on these factors, but neither distance to the wall or angle to the stimulus was associated with a statistically significant effect (see Table S1). All statistical analyses were performed in MATLAB. All experiments were conducted in accordance with Sydney University’s Animal Ethics Committee (ref. number: L04/6-2009/3/5083). All data accompanying this paper can be found at figshare.com (doi: 10.6084/m9.figshare.4903229).

RESULTS

Fig. 1A shows how the path complexity varies with respect to the time of the stimulus, averaged over all fish to obtain mean, standard deviation and standard error. A clear peak in complexity occurs directly after the introduction of the stimulus, followed by a sustained period during which the complexity is greater than before the stimulus. This shows that a fish’s movements become less predictable in response to the perceived threat and that this new movement pattern is sustained for at least 10 s after a fish’s initial change in direction. We measured the path complexity over a moving window of 1 s from the time of the stimulus until the end of the recording (10 s), and compared this with the path complexity in the period before the stimulus with a two-sample *t*-test. Over all time windows, the complexity remained elevated ($P<10^{-120}$ in all windows).

We then asked whether these movement paths were more complex depending on the distance a fish was from the stimulus. It may be beneficial for a fish that is closer to the threat to increase its path complexity because a small fish can out-manoeuvre a larger predator (Webb and De Buffrénil, 1990; Domenici, 2001). Conversely, if a fish is further away from the threat, then it may have a better chance of escape by simply fleeing directly away in order to seek cover, thereby breaking the line of sight between itself and the threat. We may therefore expect to see a greater degree of path complexity in fish that were closer to the initial threat compared with those further away. Such behavioural differences could be implemented if fish showed ‘stronger’ behavioural responses (larger speed or turning rates) to a threat at closer distances compared with when the threat came from greater distances. Fig. 1B shows that this prediction is confirmed. Whilst there was no proximity-dependent variation in path complexity prior to the stimulus [linear model (LM), $\beta=-0.0003\pm 0.0004$ (mean±s.e.), $P=0.44$], there was a negative correlation between the average complexity of the path (for a duration of 1 s after the stimulus had been released) and the distance from the threat (LM, $\beta=-0.002\pm0.0005$, $P=0.001$). Fish that were closer to the threat had more complex paths than those further away from the threat (see Figs S5 and S6 for an analysis of

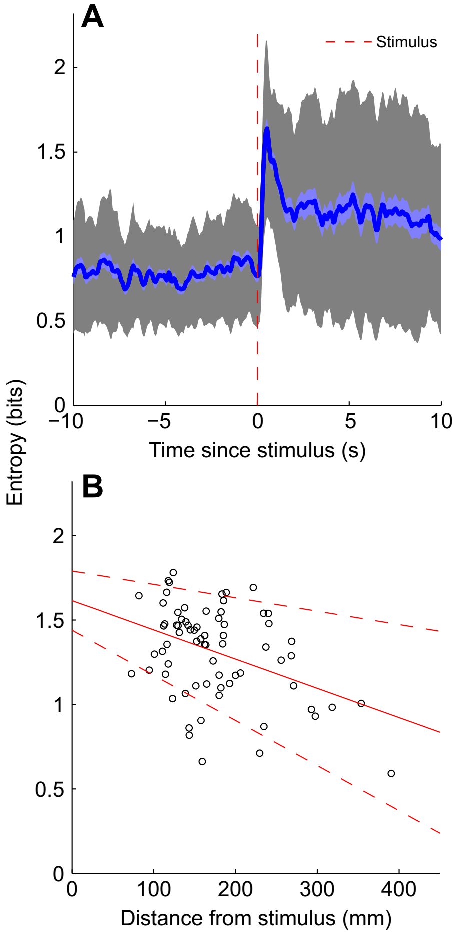

Fig. 1. The complexity of individuals’ escape paths. (A) Path complexity for the 71 experiments, before and after the stimulus, showing mean (blue line), standard error (blue shading) and standard deviation (grey shading). The path complexity rises sharply at the moment of the stimulus as the fish flees, and then remains elevated for at least 10 s afterwards, showing sustained protean behaviour. (B) Variability in path complexity of fish immediately after the stimulus with distance from the final position of the stimulus. A significant negative correlation (LM, $\beta=-0.002\pm0.0005$ s.e., $P=0.001$) shows that the fish closest to the threat exhibit the most unpredictable movement in their escape path.

the robustness of this result for increasing delay times from when entropy is recorded).

To illustrate both the change in path complexity from before the stimulus to after, and to show the dependence on spatial position relative to the threat, we plotted the average complexity of paths contained within elements of a spatial grid overlaying the experimental arena, both for a duration of 1 s before the stimulus (Fig. 2A) and for 1 s after the stimulus (Fig. 2B). It is clear that, as shown in Fig. 1, the complexity of the paths is substantially higher after the stimulus than before. Moreover, the regions of highest complexity in Fig. 2B are those closest to the position of the stimulus.

To assess whether turning rate or speed variability, or both, was responsible for this context-dependent increase in path complexity, we isolated the turning rate and speed components of the path complexity by reconstructing the escape paths to exclude speed or turning rate variation, respectively (see Materials and methods), and reran our analysis on these reconstructed escape paths. The results of analysing the reconstructed paths show that for both components, path complexity follows a temporal pattern very similar to that shown in Fig. 1, with both components rising quickly at the moment of stimulus and remaining elevated afterwards (Fig. S3). Analysis of the context dependency, as shown in Fig. 3, reveals how variability in speed and turning rate complexity are associated with the fishes' position relative to the stimulus. Speed complexity is significantly context dependent (LM, $\beta=-0.0014\pm0.0004$, $P<0.001$). Turning rate complexity is also negatively correlated with distance from the stimulus (LM, $\beta=-0.0015\pm0.0006$, $P=0.02$). There was no significant correlation between the speed complexity or turning rate complexity and the distance to the stimulus before the attack (LM, speed: $\beta=-0.0005\pm0.0004$, $P=0.28$; turning rate: $\beta=-0.0004\pm0.0005$, $P=0.38$). There was also no significant correlation between a fish's mean speed and mean turning rate either in the second before (Pearson's $r=-0.20$, $n=71$, $P=0.10$) or in the second after (Pearson's $r=0.09$, $n=71$, $P=0.47$) the stimulus entered the arena (Fig. S4).

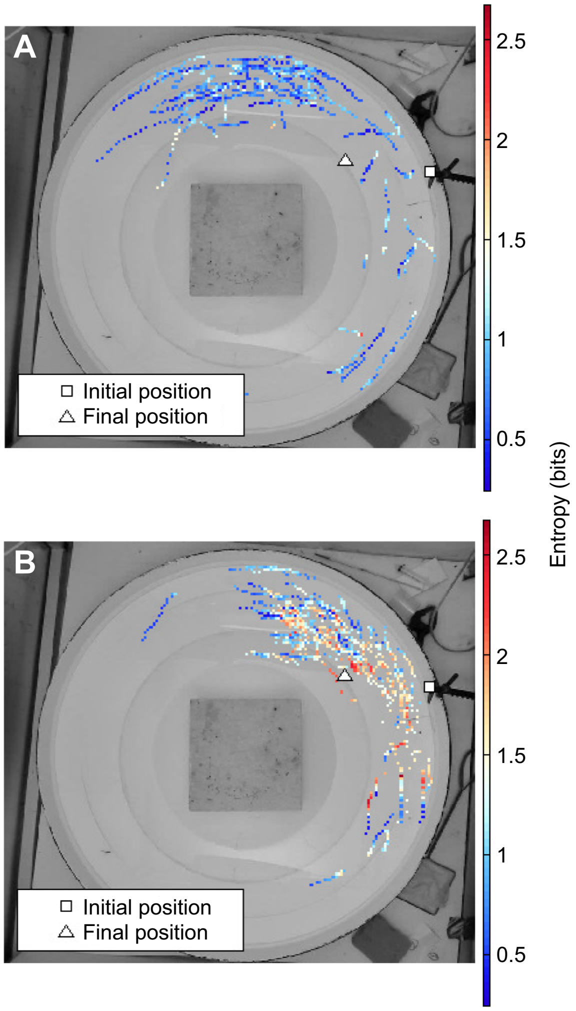

Fig. 2. Path complexity of individuals in the arena. The spatial distribution of path complexity before (A) and after (B) the stimulus. The path complexity in a spatial region (5×5 mm) is calculated as the mean complexity of the paths (for individuals on their own) passing through that region at the time of passage, over a duration of 1 s after the initial stimulus. Note, path complexity was not calculated separately within each of these 5×5 mm spatial regions. Complexity is substantially higher after the stimulus, and high complexity regions are predominantly clustered near the location of the stimulus. The initial and final positions of the stimulus are also denoted.

DISCUSSION

Following the simulated attack, a fish's path rapidly increased in complexity. The complexity of the path was dependent on how far individuals were from the threat when the attack was launched; further away from the threat, they had lower path complexity, whilst

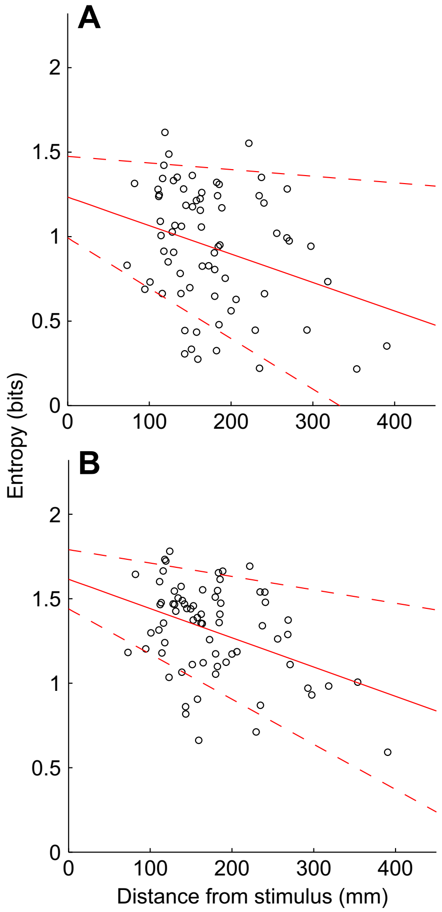

Fig. 3. Separating turning rate and speed complexity. Context dependency in turning rate (A) and speed (B) complexity after the stimulus entered the arena for individual fish. Here, the distance of the fish to the stimulus when it entered the arena (at its final position) is plotted on the *x*-axis. Turing rate and speed complexity both show a significant correlation with distance (LM, direction: $\beta=-0.0015\pm0.0006$ s.e., $P=0.02$; speed: $\beta=-0.0014\pm0.0004$ s.e., $P<0.001$).

closer to the threat, they showed higher levels of unpredictability. When partitioning the components of speed and turning rate, we found that both speed and turning rate contributed to the overall path complexity during the first second after the onset of the threat. Both speed and turning rate complexity were also context-specific, showing increased complexity when fish were further from the stimulus. This context dependency is consistent with fish showing stronger responses to the threat at closer distances.

Why might it be important to vary both speed and turning rate during an escape? If a prey were to adopt a limited range of turning rates with the same speed, then a predator would be able to intercept the prey by predicting its position in the future. Relying on turning rate changes alone, therefore, may not provide enough variation to escape predators that chase their prey. Changing speed, however, interrupts the predicted interception point, thereby making interception more difficult. Indeed, voles (*Microtus socialis*) adopt speed changes when under attack from barn owls (*Tyto alba*) by alternating between freezing and fleeing behaviours, thereby decreasing the predictability of their movements (Edut and Eilam, 2004). Because there is a trade-off between speed and the number of direction changes an individual can make (Angilletta et al., 2008), varying speed may also allow individuals to change direction during times when speed is reduced.

Here, we assessed the escape behaviour of individuals on their own, but these escape behaviours may be adapted in social settings (Herbert-Read et al., 2015). For example, other aspects of an individual's escape behaviour change in groups. Solitary herring, for example, have shorter response latencies to an attack compared with individuals in groups (Domenici and Batty, 1997). Further, the escape directions of individuals in groups are directed away from the threat in 88% of cases (Domenici and Batty, 1994). On their own, however, solitary herring move initially away from the stimulus in only 64% of cases (Domenici and Batty, 1997). Being in a group, therefore, changes the way information about a threat is perceived and responded to. Future investigations will need to consider how individuals integrate the information on the position and movements of their neighbours (Herbert-Read et al., 2011, 2013) during these escape behaviours, and how this alters an individual's path complexity.

The context-dependent escape paths we observed can simply be explained if the fish show stronger reactions to the threat when the threat is at closer distances. Indeed, this is observed in other aspects of the escape responses of fish. The instantaneous responses of prey to a threat depending on its distance show trends similar to our results. Webb (1982) classified two behavioural responses, depending on the distance to the threat: either type-I or type-II responses (Webb, 1982). Type-I responses were described as behavioural responses that showed relatively slower instantaneous speeds and non-sustained turns. These responses occurred when predators attacked prey from greater distances (Webb, 1982). Type-II responses, in contrast, occurred when fast-moving predators attacked from short-range distances, which caused the prey to increase their speed and initial turning rate (Webb, 1982). These instantaneous measures, therefore, complement our longer time-scale observations of fish's movement paths and may, in part, explain why a fish's path is more complex when closer to the threat. However, because the path complexity of an individual's movements remains at levels higher than those before the attack for at least 10 s, this demonstrates instantaneous measurements cannot fully explain why fish maintain complex movements. Because multiple attacks are often observed when predators attack prey (Handegard et al., 2012), perhaps the fish maintain complex movements to reduce the risk of being predated in possible future attacks, or to increase the chance that a predator abandons the chase. Our method highlights the need to not only investigate the initial evasive responses of prey, but also to investigate these behaviours over longer time scales.

Because the stimulus we used was above the surface of the water, and because it was relatively thin in one dimension (2.5 mm), it is unclear how the stimulus would have been perceived by the fish. Indeed, it would be particularly valuable to measure the looming or translational velocities of the stimulus, which are biologically more relevant measures for how moving stimuli are detected. This could provide an added level of detail explaining the distance-dependent escape responses that we observed. Of course, distance and angle to the stimulus will be correlated with these more detailed measures, but calculating such measures directly will provide a more sensory-based approach to understanding such escape responses.

Increasing the complexity of a path following an attack may result in predator–prey arms races becoming tipped in the favour of the prey (Dawkins and Krebs, 1979). It would be difficult for a predator to intercept a path with the highest levels of unpredictability. If prey can perform movement paths that reach these levels of unpredictability, then predators must change their attack mechanism in order to successfully capture their prey. In many cases, this could lead to predators abandoning chasing tactics and instead relying on ambush tactics. Alternatively, new predatory feeding tactics may be selected for that improve their chance of prey capture (Maresh et al., 2004). With the method we have used here to quantify the complexity of animal escape paths, we have opened new questions into how predators and prey interact over longer periods of sustained attacks.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: J.E.H.-R., A.J.W.W., D.J.T.S., R.P.M.; Methodology: J.E.H.-R., A.J.W.W., R.P.M.; Software: R.P.M.; Formal analysis: J.E.H.-R., D.J.T.S., R.P.M.; Investigation: J.E.H.-R., R.P.M.; Resources: A.J.W.W.; Data curation: J.E.H.-R., R.P.M.; Writing - original draft: J.E.H.-R., A.J.W.W., D.J.T.S., R.P.M.; Writing - review & editing: J.E.H.-R., A.J.W.W., D.J.T.S., R.P.M.; Visualization: J.E.H.-R., R.P.M.; Supervision: A.J.W.W., D.J.T.S.; Funding acquisition: A.J.W.W., D.J.T.S.

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Data availability

Data are available from figshare: doi: 10.6084/m9.figshare.4903229

Supplementary information

Supplementary information available online at
http://jeb.biologists.org/lookup/doi/10.1242/jeb.154534.supplemental

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