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Title

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Permalink

Journal

ISSN

Authors

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Publication Date

DOI

Peer reviewed

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Probabilistic analytical modelling of predator–prey interactions in fishes

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Predation is a fundamental interaction between species, yet it is largely unclear what tactics are successful for the survival or capture of prey. One challenge in this area comes with how to test theoretical ideas about strategy with experimental measurements of features such as speed, flush distance and escape angles. Tactics may be articulated with an analytical model that predicts the motion of predator or prey as they interact. However, it may be difficult to recognize how the predictions of such models relate to behavioural measurements that are inherently variable. Here, we present an alternative approach for modelling predator–prey interactions that uses deterministic dynamics, yet incorporates experimental kinematic measurements of natural variation to predict the outcome of biological events. This technique, called probabilistic analytical modelling (PAM), is illustrated by the interactions between predator and prey fish in two case studies that draw on recent experiments. In the first case, we use PAM to model the tactics of predatory bluefish (*Pomatomus saltatrix*) as they prey upon smaller fish (*Fundulus heteroclitus*). We find that bluefish perform deviated pure pursuit with a variable pursuit angle that is suboptimal for the time to capture. In the second case, we model the escape tactics of zebrafish larvae (*Danio rerio*) when approached by adult predators of the same species. Our model successfully predicts the measured patterns of survivorship using measured probability density functions as parameters. As these results demonstrate, PAM is a data-driven modelling approach that can be predictive, offers analytical transparency, and does not require numerical simulations of system dynamics. Though predator–prey interactions demonstrate the use of this technique, PAM is not limited to studying biological systems and has broad utility that may be applied towards understanding a wide variety of natural and engineered dynamical systems where data-driven modelling is beneficial.

1. Introduction

Predation is critical to the structure of populations and has guided the evolutionary fate of myriad species. Despite its importance in biology, investigators have struggled to formulate a predictive body of theory for understanding the behaviours that succeed in the survival or capture of prey. It is consequently unclear what traits of a predator or prey are most important to predation. This challenge has been met through the development of analytical models that articulate tactics and predict the motion of these animals. However, it is difficult to reconcile these predictions with kinematic measurements due to the highly uncontrolled and coupled nature of behavioural interactions between predator and prey. The aim of the current study is to advance our understanding of the behaviour of predation through the introduction of an analytical approach that incorporates kinematic measurements of natural variation into analytical models of predator and prey tactics.

The work here is motivated by the importance of predation in the survival of a species. Rather than studying the growth rate of species, we instead take an individual-centric approach where we seek to quantify the expected value of a

metric of success in the predator–prey interaction. We demonstrate the utility of our approach, called probabilistic analytical modelling (PAM), by modelling predator–prey interactions in fishes that have been observed experimentally. Measurements of kinematic features such as speed, flush distance (i.e. the escape or alert distance) and escape angles from experiments combined with dynamical modelling and probabilistic analysis predict the outcomes of biological events in ways that experiments or modelling alone cannot.

Hypothetical tactics of predators and prey have been previously formulated with analytical pursuit–evasion models. These models predict the trajectories of individuals [1–3], or the swarming behaviour of one target and many pursuers [4,5], as particles capable of responding to the state of the opposing animal according to a behavioural algorithm [6–9]. Owing to the transparency of analytical mathematics, it is possible to resolve the parameters in these algorithms that optimize a particular aspect of performance. For example, the classic homicidal chauffeur game model was successfully used to formulate the direction of the escape response by prey fish that maximizes the distance from a predator [10,11]. This model has been invoked in the interpretation of numerous experimental studies on prey fish [12–16].

However, attempts at reconciling theory with experimentation demonstrate some of the limitations of existing theory. The homicidal chauffeur model assumes that predator and prey maintain a fixed heading and velocity and that the prey senses the predator's speed and heading with perfect accuracy. These assumptions seem unlikely to hold true in most piscivorous interactions and it is, therefore, unclear to what extent measured deviation from predictions may be attributed to violations of the model's assumptions, fish using a different tactic, or other natural variation in behaviour. As a consequence, it is not clear whether or not prey fish escape optimally with respect to some metric (e.g. distance from the predator).

The effects of natural variation have been considered by computational models that include stochasticity. Such data-driven models include those of fish schools that respond to a predator [17] and a schooling model that investigates how perturbations among a small number of agents affects the behaviour of the school at large [18]. Certain classes of stochastic pursuit–evasion games have even been solved [19] and the importance of not using deterministic models in stochastic systems is highlighted in a model of the growth rate of feeding fish [20]. In work on specific species, data-driven techniques with stochastic or probabilistic elements are used to model the fast-turning dynamics of zebrafish [21], the probability of capture for suction feeding sunfish [22], the predation by the exotic shrimp species *Dikerogammarus villosus* [23], and the dynamics of the bacterial predation in soil [24]. On a macro-scale, predator–prey population dynamics in the sense of Lokta–Volterra [25] are modelled with stochastic components to the birth and death rate of the species [26] and with data fitting techniques that generalize the local predator–prey interactions to the population dynamics as a whole [27].

Although perhaps more predictive than a classic analytical model, the above data-driven models lack the advantages of analytical analysis for formulating tactics that optimize some payout. The same disadvantage is apparent in a Monte Carlo approach to pursuit–evasion models. A Monte Carlo method yields distributions of numerical results from batches of deterministic trials that draw parameter values from random-number generation according to

measured probability distributions [28]. This approach is similar in concept to the present approach, but its numerical execution lacks the advantages of an analytical approach.

The proposed approach, PAM, allows for a consideration of natural variation in a pursuit–evasion model by combining kinematic measurements with dynamical modelling that articulates predator or prey tactics. This approach may be executed in four steps. First, a model of the dynamics of the predator/prey interaction is either chosen from existing pursuit–evasion models or developed to more specifically address the behaviour seen in experiments. Second, for each of the probabilistic parameters appearing in the model, a probability density function (PDF) is fit to measurements. Third, the key metric that measures the success of either the predator or prey is selected and expressed mathematically. Tools from probability theory are applied to calculate the expected value of the key metric as a function of the PDFs of the model parameters. Finally, the means of the PDFs are varied and the expected value of the key metric is recalculated to determine the relative influence of each parameter. This procedure reveals which factors are most important to either predator or prey survival, taking into account the random distribution of parameter values seen in experimental observations. Though predator–prey interactions motivated the development of this technique, PAM is, in fact, applicable to any process that can be examined by data-driven mathematical modelling.

The paper proceeds as follows. Section 2 provides technical background in pursuit dynamics and probability theory and introduces two case studies of fish predator–prey interactions. Section 3 presents the general PAM approach used to analyse each experimental dataset in order to determine the most important tactical factors in predator–prey interactions. Section 4 applies PAM to a case study of the pursuit tactics of bluefish predators and §5 uses the methodology on a case study on the evasion tactics of zebrafish prey. Although the primary data analysed in these two cases is based on two previous experimental studies [28,29], the results reported here can be verified using the statistical data provided in this work. Section 6 summarizes the results and describes ongoing work.

2. Background

2.1. Pursuit dynamics

The literature on pursuit is multi-disciplinary, with works coming from both the animal behaviour [7,30–32] and missile guidance [6,33,34] communities. Owing to this mixing of disciplines and a lack of formalization in the field, there are many (sometimes conflicting) terms used to describe various pursuit tactics. In *pure pursuit* (PP), also sometimes called *tracking* or *classical pursuit*, a pursuer aligns its velocity vector with the line of sight (LOS), which is the vector from the pursuer to the target's current location and is used by many predators [6,35].

In *deviated pure pursuit* (DPP) (i.e. *constant bearing pursuit* or *constant aspect pursuit*), the pursuer aligns its velocity vector a fixed angle away from the LOS such that it leads (or lags) the target. Certain fish [30], insects [35], dogs [36] and humans [37] exhibit this tactic in their pursuit trajectories. The special case where the target is not turning or changing speed and the pursuer's lead angle is such that it moves in a straight line for the entire pursuit phase is sometimes called *interception*.

In *constant absolute target direction* (CATD) *pursuit* (also known as *motion camouflage, parallel navigation* or *constant bearing*), the pursuer moves in such a way that the LOS angle stays fixed with respect to some inertial reference frame. This tactic has the effect of masking the pursuer's transverse movement from the perspective of the target, because the pursuer appears only to increase in size. Certain dragonflies [31], bats [32] and falcons [38] use this tactic. In the case of a non-manoeuvring target, CATD pursuit is equivalent to constant bearing pursuit, but the converse is true only in the case of interception. A common technique to actualize one of these geometrical tactics into a control law for a physical system with dynamics is proportional navigation [33], though other techniques exist [6,39].

2.2. Probability theory

Probability theory provides a mechanism to analytically account for inherently variable behavioural measurements observed in predator–prey interactions. The probability that a random variable X has value less than x is described by the cumulative distribution function $F_X(x) = P(X \le x)$ [40]. The PDF of the same random variable describes how often values occur and is given by $f_X(x) = dF_X(x)/dx$. Many techniques and toolboxes exist for fitting PDFs to a dataset [41,42].

The expected value of a random variable X with probability density $f_X(x)$ is [40]

$$E[X] = \int_{-\infty}^{\infty} x f_X(x)\, dx. \tag{2.1}$$

The expected value of a function $Y = h(X)$ of random variable X with probability density $f_X(x)$ is [40]

$$E[Y] = \int_{-\infty}^{\infty} h(x) f_X(x)\, dx. \tag{2.2}$$

Additional results from probability theory necessary for the work herein and not contained in the references are in the appendix.

2.3. Case study 1: bluefish

Piscivorous interactions may largely be described by two-dimensional kinematics, but exhibit a diversity of tactics that have the potential to vary with the habitat and the physiology of a fish species. Bluefish (*Pomatomus saltatrix*) are voracious pelagic fish predators that pursue prey at a high speed. This species exhibits predatory behaviour in an aquarium with motion that is largely two dimensional and is therefore conducive to single-camera kinematic measurements. As detailed in a separate study [29], the high-speed kinematics were measured for bluefish (approx. 30 cm in length) as they preyed upon smaller prey fish, mummichog (*Fundulus heteroclitus*, approx. 5 cm). These experiments introduced an individual prey into the centre of a large cylindrical aquarium (diameter = 6 m), which contained all of the predators. Kinematic measurements were performed for the prey and predator that first struck at the prey. Inherent in this decision is the assumption that the successful predator's trajectory is not affected by the presence of other predators in the area. The validity of this assumption is addressed in §4. These measurements consisted of a manual frame-by-frame tracking of the rostrum of each fish from the moment that both appeared in the camera's field of view until the predator's strike. The mummichog did not attempt an escape

when pursued by bluefish, but rather maintained a relatively straight path and consistent speed. The trajectories of predator and prey were recorded for 70 experimental trials. The dynamical model of bluefish predation presented in §4 takes advantage of the largely non-manoeuvring prey, allowing for a DPP representation with only the LOS range and angle as state variables.

2.4. Case study 2: zebrafish

Zebrafish adults (approx. 2.5 cm) prey on larvae (approx. 4 mm) of the same species under laboratory conditions [43]. However, unlike the mummichog preyed upon by bluefish, zebrafish larvae generally remain stationary until initiating an escape response at a certain point during the predator's approach [16]. This response allows for a consideration of the evasion tactic of a prey fish that can be measured and modelled. The kinematic data were previously reported from experiments in a hemispherical aquarium (diameter = 8.5 cm), where the predator attempted multiple strikes at the prey until successful [28]. Within 1 s of initiating an escape, the prey ceased swimming and were stimulated to escape again when approached by the predator. The predator approached the prey at a constant speed, well below the prey's maximum escape speed. This approach was consistent with a PP tactic, such that the predator's heading was directed towards the instantaneous position of the prey. These interactions repeated for as many as 20 approaches in experiments performed in a relatively small aquarium and were previously characterized by iterating a model of a single interaction using a Monte Carlo technique [28].

The dynamic model of the zebrafish interaction presented in §5 is an example of a hybrid system. A hybrid system is a dynamical system that has a combination of continuous- and discrete-time behaviour [44,45]. Hybrid systems often involve the discrete switching between sets of dynamics, such as a thermostat, or a discrete jump in states, such as a bouncing ball. Stochastic hybrid systems are those that have non-deterministic dynamics or non-deterministic conditions on the state switching [46]. Here, a hybrid system is needed to model the switch between freezing and escaping behaviour.

3. Probabilistic analytical modelling general method

We now present the general PAM procedure used to determine which parameters in a given predator–prey interaction are most critical to survival.

1. Choosing a dynamic model. The first step is to analyse the experimental kinematic data to determine the dynamics of the system. A catalogue of standard pursuit tactics and their dynamical models may be useful [6,7], see §2.1. In more complicated cases, where the prey is highly responsive to the actions of the predator, a differential-game setting may be required [47].

The chosen model need not exactly predict the actions of the predator and prey seen in experiments, but it should capture the essential attributes of their behaviour. For example, many of the standard pursuit models assume constant speed of the predator and prey, which is not the case in a biological system. This assumption may be tolerable (as with the bluefish case study in §4) unless either the predator or prey

exhibit some specific speed-changing behaviour (such as the starting and stopping of the larvae's motion in response to the zebrafish in §5).

If the predator–prey interaction is well modelled by a dynamical system from the literature (as it is in §4), then deriving an analytical expression for the key metric may be trivial or already available. If a more non-traditional model is required to describe the behaviour (as in §5), then the development of the model and the derivation of the expression for the key metric may be an iterative process.

2. Fitting probability densities to the experimental data. Once a model has been selected, each of the parameters in that model are fit from the experimentally observed dataset. These parameters may include predator or prey speeds, angles, capture rates etc. It may be advantageous to model certain parameters as deterministic and others as probabilistic to simplify the expression of the expected value of the key metric. For example, in §4, the predator and prey speeds are treated as random variables, whereas in §5, they are deterministic because more interesting behaviour in the prey species arises from variations in sensing range.

Many techniques exist for fitting PDFs to datasets [41,42]. A particular form of the PDF for each parameter is not required for the following steps (e.g. it need not be normally distributed) and that fact is a strength of this work. In certain cases, deterministic functions may be fit to data, like the success rate of strikes as a function of distance in §5.

3. Choosing a key metric. The key metric will be a measure of the success of the predator or prey in either the predation or escape behaviour. In many cases, such as for probability of capture, the predator's goal is to maximize the metric and the prey's goal is to minimize it.

An analytical expression of the key metric is required to calculate its expected value. The expression is derived from the model of the predator/prey interaction and both the expression itself and the steps to derive the expression may be unique to each model and metric. Some component of the system dynamics may need to be directly integrated and numerical integration may not be sufficient. For this reason, concurrent or iterative development of the model and the expression of the key metric may be required to modify the model into an integrable form.

4. Finding the expected value of the key metric. Depending on the form of the expression of the key metric, a direct application of the multivariate extension of equation (2.2) will provide the expected value, as is the case in §4. For more complicated expressions, something akin to what is done in §5 may be required, where conditional statements are incorporated into the calculation of the expected value.

5. Parameter perturbation analysis. To study the relative effect each of the parameters in the model has on the expected value of the key metric, we employ a scheme similar to that used in [28], where the expected values of the probabilistic parameters are varied by shifting the terms within the PDFs. In [28], the varied PDFs were tested in a Monte Carlo framework to recalculate the expected value of the key metric from a multitude of simulations. In the work described here, the expression for the expected value of the key metric need only be re-evaluted with the varied PDFs, taking advantage of the inclusion of the system dynamics in the key metric.

The expected value of the key metric as a function of the change of each parameter from its nominal value reveals
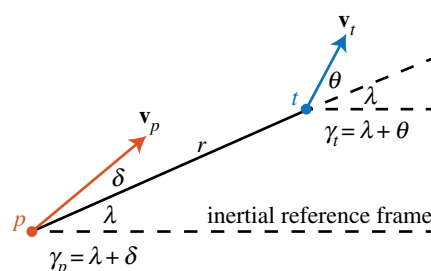

Figure 1. Pursuit kinematics for predator (p, red) and prey (t, blue). The swimming direction of both animals are defined by the velocity of prey ($\mathbf{v}_t$) and predator ($\mathbf{v}_p$), relative to the range vector (r, at angle λ), specified by the bearing of predator (δ) and prey (θ). The heading (γ) of each animal is defined relative to the inertial reference frame. (Online version in colour.)

which parameter most greatly influences the key metric and, therefore, the survival of either the predator or prey. Though the PAM technique was developed for predator–prey interactions, it is applicable to examine metrics for any dynamical process with natural variation in the parameters.

4. Bluefish case study

This section describes the application of PAM to examine the predatory behaviour of bluefish as they preyed upon mummichog [29].

Deviated pure-pursuit dynamics. Figure 1 defines the planar pursuit geometry used in this case study. The vector of length r between the predator and the prey is known as the LOS and is inclined from the inertial reference frame by an angle λ. The predator's velocity vector $\mathbf{v}_p$ is inclined from the LOS by the pursuit (deviation) angle δ and likewise the prey's velocity $\mathbf{v}_t$ is inclined by θ. The velocity magnitudes (i.e. speeds) are denoted $v_p > 0$ and $v_t > 0$. The angle of the velocity vectors from the inertial frame are γ_p and γ_t for the predator and prey, respectively.

To verify that the bluefish are using DPP, we compared simulations of the DPP dynamics to the experimental trajectories. Comparisons were very favourable even without accounting for predator–predator interactions. Figure 2 shows three examples of these comparisons, where the simulated trajectories obey the following dynamics:

$$
\left.
\begin{aligned}
\dot{x}_p &= v_p \cos \gamma_p, \\
\dot{y}_p &= v_p \sin \gamma_p, \\
\dot{\gamma}_p &= k(\lambda + \delta^* - \gamma_p) = k(\delta^* - \delta)
\end{aligned}
\right\} \quad (4.1)
$$

and $\quad v_p(t) = $ measured predator speed at time t,

where (x_p, y_p) is the predator position, $k > 0$ is the scalar feedback gain, and δ^* is the desired pursuit angle. With γ_p as a control input, these dynamics use only the geometric angle δ as feedback, a value that may be available to the bluefish from their visual system [30]. In the experimental data, the predator's speed v_p varies within a pursuit. Thus, in the simulated trajectories (e.g. figure 2) the DPP tactic is used for the predator steering, given the experimentally measured values of speed. The particular pursuit angle δ^* used in (4.1) is unique to each trial and was found by sweeping through values $\delta^* \in (-\pi, \pi]$ and choosing the δ^* that best matched the experimental trajectories in the least-squares sense.
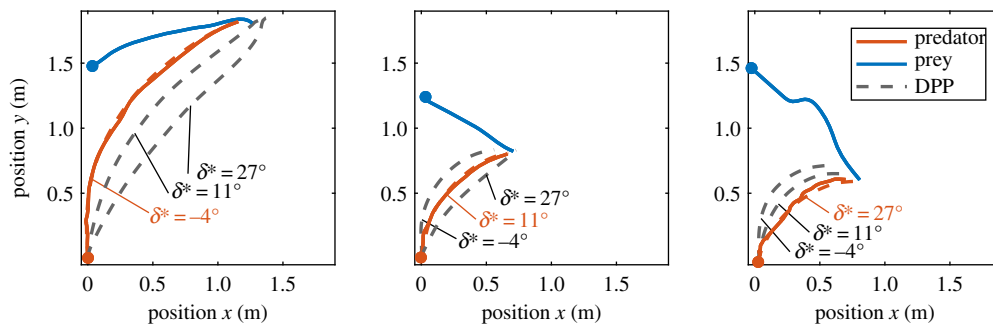
Figure 2. Trajectories of predator and prey for three representative experiments. Dotted trajectories are those generated by the deviated pure pursuit (DPP) control eqn (4.1) with $\delta^* = -4°$, $11°$ and $27°$, which were the best match for these trials from left to right, respectively. (Online version in colour.)
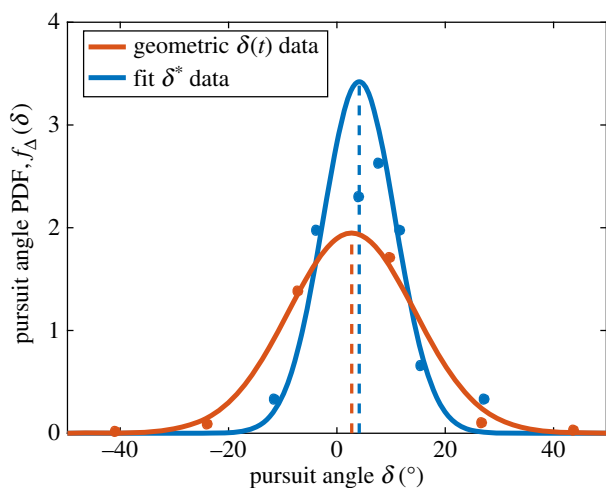

Figure 3. PDF for the pursuit angle δ fit from experimental data. Geometric $\delta(t)$ data are determined from the predator heading γ_p and line of sight angle λ at each time step. Fit δ^* data are the angles in dynamics (4.1) that best match the fish trajectories. (Online version in colour.)

Experimental data fitting. Three probabilistic parameters are needed to calculate the expected value of the time to capture as seen below in the key metric section. The pursuit angle δ as calculated by the geometry in figure 1 is well represented by a normal distribution. However, since $\delta \in (-\pi, \pi]$, we use a von Mises distribution, which is often referred to as the wrapped normal distribution. Figure 3 shows two PDFs given by

$$f_\Delta(\delta) = \frac{1}{2\pi I_0(\kappa_\delta)} \exp\left(\kappa_\delta \cos(\delta - \mu_\delta)\right), \quad (4.2)$$

where I_0 is the modified Bessel function of order 0, μ_δ is the mean value and $\kappa_\delta \geq 0$ is a term that represents the spread of the distribution with $\kappa_\delta = 0$ corresponding to a uniform distribution. The first PDF is fit from the geometrical $\delta(t)$ at every time step across all experiments and the second is fit from the δ^* value associated with each trial from dynamics (4.1). The $\delta(t)$ PDF has much more variance because the bluefish do not perfectly track the δ^* values and oscillate about them in each trial. Values for the δ^* fit parameters are used in this case study (the result is nearly identical in either case) and are given in table 1.

The probability densities for the speed of the predator and prey are not independent because although the prey is largely unresponsive to the actions of the predator, it is unclear whether or not the predator adjusts its speed in response to the prey. A bivariate lognormal density is fit to the dataset of (v_p, v_t) pairs taken at every time step across all

experimental trials. Let $L(v_p, v_t, \mu_v) = [\ln v_p, \ln v_t]^T - \mu_v$. Figure 4 shows the joint PDF

$$f_{V_p,V_t}(v_p, v_t) = \frac{1}{2\pi\sqrt{\det\Sigma_v}} \exp\left(-\frac{1}{2}L(v_p, v_t, \mu_v)^T\Sigma_v^{-1}L(v_p, v_t, \mu_v)\right), \quad (4.3)$$

where μ_v and Σ_v are given in table 1.

Key metric. In the experimental set-up, many bluefish simultaneously begin pursuit when the prey fundulus is dropped into the arena. As the bluefish are nearly always successful in capturing the prey once they reach it, the first predator to reach the prey received the reward. Therefore we choose the key metric to be the time to capture.

Assume a constant speed for the predator and a non-manoeuvring prey, meaning the prey moves with constant speed and direction. Though this it not strictly the case for the experimental data, we seek to examine the effect of pursuit angle δ and so we do not study the effect of changing speed during a pursuit. Additionally, assume that the predator maintains a constant pursuit angle δ throughout its trajectory. The predator speed, prey speed and pursuit angle are considered as random variables.

With these assumptions, the dynamics of the DPP system in terms of the rate of change of the LOS range r and angle λ shown in figure 1 are [6]

$$\dot{r} = v_t \cos\theta - v_p \cos\delta$$

and $\quad -\dot{\lambda} = \dot{\theta} = \frac{1}{r}(-v_t \sin\theta + v_p \sin\delta),$

where $\dot{\lambda} = -\dot{\theta}$, because the prey is non-manoeuvring. Using these dynamics, the time to capture is [6]

$$t_c(r_0, \theta_0, v_p, v_t, \delta) = r_0 \frac{v_p + v_t \cos(\theta_0 + \delta)}{(v_p^2 - v_t^2)\cos\delta}. \quad (4.4)$$

Expected value of key metric. For two random variables X and Y and a nonlinear function $Z = g(X, Y,)$ it is not true, in general, that $E[Z] = g(E[X], E[Y])$ [40]. Since three of the parameters in (4.4) are random variables, we must instead calculate the expected value by using the multivariate extension of (2.2):

$$E[T_c] = \iiint_{-\infty}^{\infty} t_c(r_0, \theta_0, v_p, v_t, \delta)f_{V_p,V_t}(v_p, v_t)f_\Delta(\delta)\,dv_p\,dv_t\,d\delta, \quad (4.5)$$

which assumes δ is independent from v_p and v_t.

Parameter perturbation analysis. To determine which parameters have the greatest effect on the time to capture t_c, we use the technique described in §3. Figure 5a shows the

Table 1. Parameters of the bluefish pursuit model. Pursuit angle δ has a von Mises distribution with PDF $f_\Delta(\delta)$. The predator speed v_p and prey speed v_t form a bivariate lognormal PDF $f_{V_p,V_t}(v_p, v_t)$. The given parameters correspond to mean speeds of 1.38 and 0.95 m s^{-1} for the predator and prey, respectively. Initial conditions are deterministic with nominal values as given.

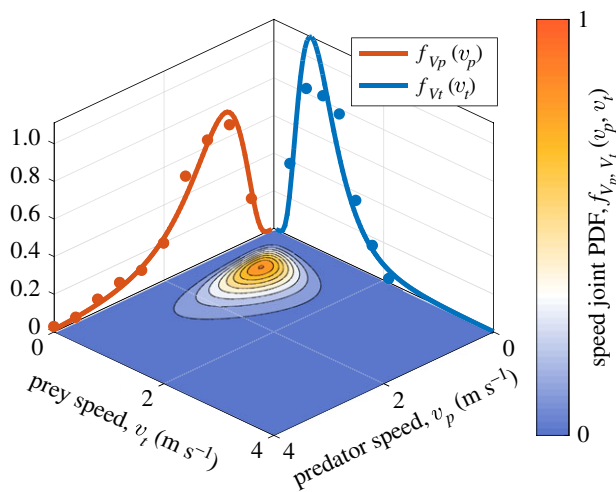| probabilistic parameters	δ	pursuit angle	$\mu_\delta = 0.0720$ rad
			$\kappa_\delta = 73.8049$
	v_p	predator speed	$\mu_v = \begin{bmatrix} 0.1565 \\ 0.5286 \end{bmatrix}$
	v_t	prey speed	$\Sigma_v = \begin{bmatrix} 0.2849 & 0.1070 \\ 0.1070 & 0.9147 \end{bmatrix}$
initial conditions	r_0	range	1 m
	θ_0	prey heading	$\pi/2$ rad

Figure 4. Joint PDF for predator speed v_p and prey speed v_t shown as a contour plot. Marginal PDFs are shown in blue and orange in the vertical axis. (Online version in colour.)

result of this process, in comparison to a deterministic evaluation of (4.4) directly using $E[V_p]$, $E[V_t]$ and $E[\Delta]$. Increasing the prey speed or decreasing the predator speed has a much less pronounced effect on $E[T_c]$ when compared with the deterministic technique. This effect is because the deterministic case considers only single values of v_p or v_t that may become very close as either is varied, causing t_c to become large. The probabilistic case balances this effect by considering all possible values of v_p and v_t according to their likelihood from (4.3). Even if $E[V_p]$ and $E[V_t]$ are very close, there are still many other values that are accounted for by (4.5). The nominal initial conditions used in this plot are $r_0 = 1$ m and $\theta_0 = \pi/2$ rad.

Figure 5b shows an extended variation of the pursuit angle δ from its small nominal value of 4.13°. We see that there exists an optimal pursuit angle much higher than the pursuit angle most often used by the bluefish. This optimal angle corresponds to the intercept tactic (see §2.1). Since the bluefish do not appear to be optimizing this metric, we discuss alternative explanations below.

Discussion. The deterministic versus probabilistic study of the effect of varying the parameters yields different, yet qualitatively consistent results as seen in figure 5. Though the unperturbed (0% change from experimental parameters) value of time to capture is incorrect, the deterministic study yields the correct trends near the nominal values, but does not accurately predict time to capture as the parameters are

varied further. For larger deviations, the probabilistic study shows the expected effect on the time to capture t_c.

As seen in the δ curve in figure 5a, increasing/decreasing the pursuit angle δ has very little effect on the time to capture, because the bluefish most often use small, but non-zero, pursuit angles (figure 3). Why the bluefish use a DPP tactic over a PP tactic (the $\delta = 0$ case) when it yields such small changes in capture time is not clear. The analysis shows that a time-optimal pursuit angle exists (figure 5b), though the bluefish operate far from its value. DPP may present a tactical advantage for a more evasive prey than the prey presently considered. For example, a faster prey might prompt the bluefish to increase δ such that their swimming trajectory more closely resembles the CATD tactic (see §2.1). Alternatively, DPP may indicate a constraint or bias on the sensorimotor system of the bluefish. Bluefish may more quickly process the position of the prey when it is present in the visual field of a single eye, which is facilitated by a non-zero value for δ. In most cases, the predator chose to fix the prey in the eye on the side that leads the prey velocity ($\delta > 0$), which does slightly reduce capture time compared to the negative of that angle.

5. Zebrafish case study

The second PAM case study considers prey evasion tactics in larval zebrafish pursued by adult zebrafish [28]. The prey, in this case, attempts to escape by accelerating to a speed that is faster than the predator, as described in §2.4.

To calculate the key metric for this case study, a one-dimensional hybrid system model of the dynamics is formulated. The continuous part of the hybrid system describes the approach of the predator and the escape behaviour of the prey, whereas the discrete part handles the switching of parameters between repeated approaches and the onset of escaping behaviour.

Hybrid pursuit model. Among pursuit tactics [6–8], PP is best represented by a one-dimensional model since the predator always moves directly towards the prey and the distance between them is of prime importance.

The distance between the predator and prey at time t is $r(t)$. The predator will attempt a strike if $r(t)$ is less than the strike distance s. The prey begins its escape if $r(t)$ is less than its sensing range (flush distance) l. The prey escapes for η seconds, reaching its maximum speed v_t at a fraction χ of its escape time. $C(s)$ is the probability of a successful strike as a function of strike distance s and is experimentally
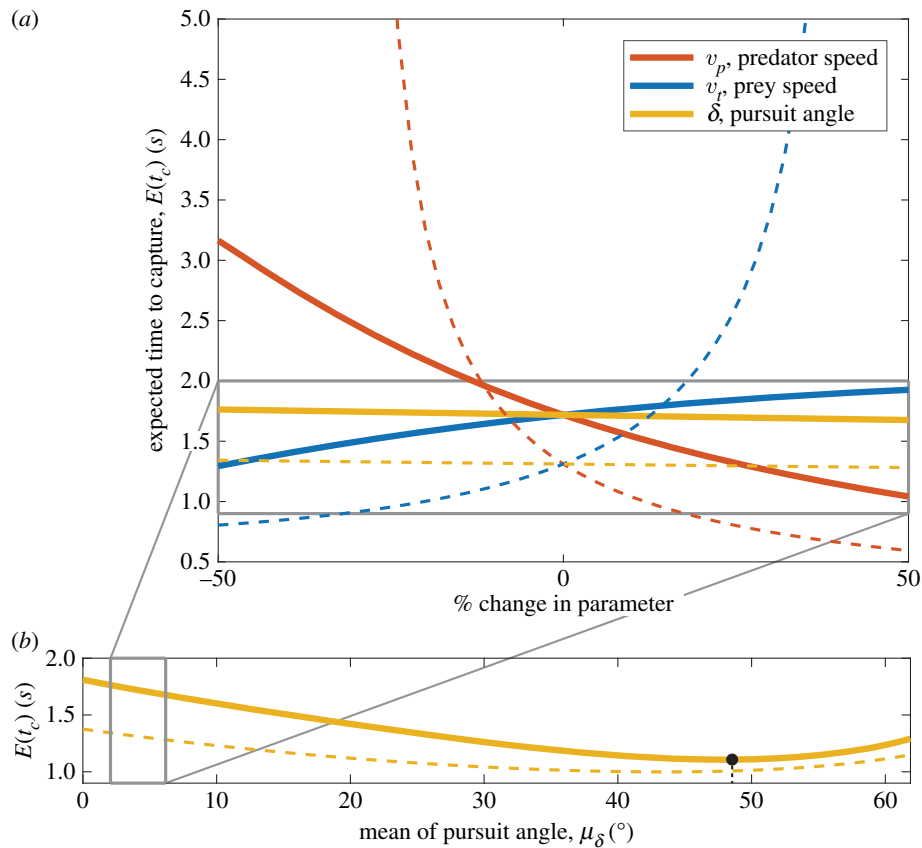
Figure 5. (a) Probabilistic parameter variation for the bluefish case study (solid). Dashed lines are those from deterministic perturbation analysis. (b) Extended variation for the pursuit angle δ with the black circle showing the minimum time to capture. The region outlined in grey is shown in (a). (Online version in colour.)

Table 2. Parameters of the model for the zebrafish case study. Probabilistic parameters have lognormal probability density functions $f_S(s)$, $f_L(l)$ and $f_H(\eta)$. $C(s)$ is a sigmoidal function of the form $C(s) = [1 + \exp(-\rho(s - \rho_0))]^{-1}$.

probabilistic parameters	s	strike distance of predator	$\mu_s = -4.980$
			$\sigma_s = 0.448$
	l	sensing distance of prey	$\mu_l = -4.546$
			$\sigma_l = 0.587$
	η	escape duration of prey	$\mu_\eta = -1.369$
			$\sigma_\eta = 0.552$
deterministic parameters	v_p	predator speed	0.13 m s^{-1}
	v_t	maximum prey speed	0.4 m s^{-1}
	χ	fraction of η when u is reached	0.2
deterministic function	$C(s)$	strike success chance	$\rho = -0.573$
			$\rho_0 = 5.20$

determined. Table 2 summarizes the parameters used in the model and includes their values for this case study.

Assume that the predator reaches its maximum speed v_p sufficiently far from the prey so that predator acceleration may be ignored. The prey remains stationary until it detects the predator, that is, until $r(t) \leq l$, the sensing distance of the prey. Once the predator is detected, the prey escapes with a sawtooth velocity profile, as shown in figure 6. This type of velocity profile is general to many startle responses seen in nature where the prey quickly flees only to come to rest again a short time later [28].

Figure 7 illustrates the hybrid dynamics of this non-deterministic system for one or more approaches. The approach number $a_n = n$ counts the number of times the prey

has begun escaping from the predator. The time since observation begins is t. The time from when approach a_n begins is $t^{(n)} = t - t_0^{(n)}$, where $t_0^{(n)}$ is the time when a_n increments. Additionally, on approach n, each of the probabilistic parameters $s^{(n)}$, $l^{(n)}$ and $\eta^{(n)}$ are redrawn from their densities, $f_S(s)$, $f_L(l)$ and $f_H(\eta)$, respectively. Figure 8 shows a sample trajectory of the dynamics using the case-study data.

Experimental data fitting. All of the parameters in table 2 were experimentally determined or fit in [28]. The probabilistic parameters have lognormal PDFs with the form

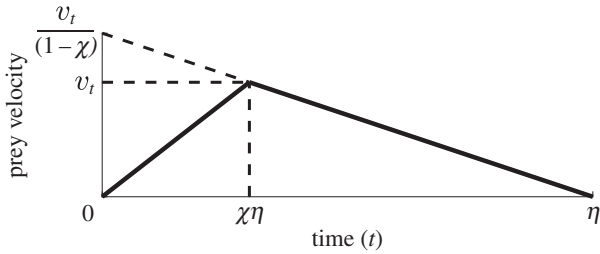$$f_X(x) = \frac{1}{x\sqrt{2\pi\sigma_x^2}}\exp\left(-\frac{(\ln x - \mu_x)^2}{2\sigma_x^2}\right).$$

Figure 6. Prey velocity profile (v_t) after detecting the predator. The prey escape duration is η; it reaches its maximum speed at fraction χ of the escape duration.
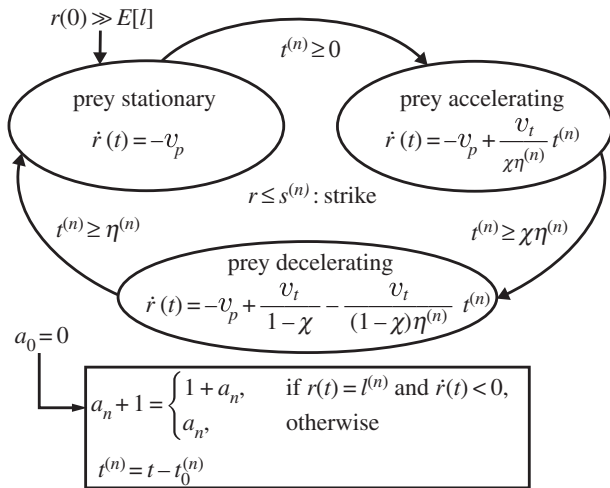

Figure 7. Non-deterministic hybrid system model of predator–prey interaction. The box represents the discrete dynamics and the ellipses represent continuous dynamics. Probabilistic variables are redrawn from their respective PDFs each time the approach number a_n is incremented.

The strike probability of success has the form $C(s) = [1 + \exp(-\rho(s - \rho_0))]^{-1}$. Though the experiments showed some variation in the maximum speed of the predator and prey, here we treat them as constants because we seek to study the more interesting fleeing behaviour of the prey.

Key metric. Probability of capture has relevance to both the predator and prey, one seeking to maximize it and the other to minimize it. The goal is now to analyse the hybrid system to derive an expression for the expected value of the probability of capture on approach and the probability of survival after n approaches.

Expected value of key metric. For the prey to be captured, two conditions must be met. First, the minimum distance $r^{(n)}$ must be less than the strike distance. If $r^{(n)}$ is not less than $s^{(n)}$, then no other point on the trajectory will be. This condition states that a strike will be attempted, though not where the strike will occur. Second, the strike must be successful. This condition is given by the function $C(s)$, which gives the probability of success of a strike at distance $s^{(n)}$. Thus for the predator–prey interaction described by the dynamics in figure 7, the probability of capture on approach is

$$P_{\text{CoA}} = E[C(s)], \text{ given } r \leq s.$$

Critical to this analysis is finding the minimum distance $r^{(n)}$ between the predator and prey. With the goal to find the minimum distance r on a single approach, we restrict our analysis to the interval $t^{(n)} \in [0, \eta^{(n)}]$. The first of two possibilities where r may achieve a minimum is $\underline{r_1}$ during the prey accelerating

phase in figure 7, when $\dot{r} = 0$ at $t^{(n)} = v_p \chi \eta^{(n)}/v_t$. The second possibility is $\underline{r_2}$ during the prey decelerating phase in figure 7, which occurs at the end of the interval, $t^{(n)} = \eta^{(n)}$. The minimum on the interval is then $\underline{r} = \min(\underline{r_1}, \underline{r_2})$.

To find $\underline{r_1}$, from figure 7, we have

$$\dot{r}(t) = -v_p + \frac{v_t}{\chi\eta}t, \quad r(0) = l \tag{5.1}$$

on the interval $t \in [0, \chi\eta]$, where we dropped the superscripts on $t^{(n)}$, $\eta^{(n)}$ and $l^{(n)}$ as we are considering only a single approach and each approach is an independent event. Integrating directly and evaluating at $\underline{t} = v_p(\chi\eta/v_t)$, the local minimum is

$$\underline{r_1}(\eta, l) = -\frac{v_p^2 \chi}{2v_t}\eta + l. \tag{5.2}$$

The second possible minimum, $\underline{r_2}$, occurs at the end of the entire escape phase shown in figure 6 at $\underline{t} = \eta$. The distance travelled by the predator and prey during this time are $v_p\eta$ and $v_t\eta/2$, so

$$\underline{r_2}(\eta, l) = \left(\frac{v_t}{2} - v_p\right)\eta + l, \tag{5.3}$$

The two possible minima $\underline{r_1}$ and $\underline{r_2}$ are each a linear combination of η and l, so the joint PDF is expressed in terms of $f_H(\eta)$ and $f_L(l)$ as [48]

$$f_{\underline{R_1 R_2}}(\underline{r_1}, \underline{r_2}) = \frac{1}{ad - bc}f_H\left(\frac{d\underline{r_1} - b\underline{r_2}}{ad - bc}\right)f_L\left(\frac{-c\underline{r_1} + a\underline{r_2}}{ad - bc}\right), \tag{5.4}$$

where $a = -v_p^2\chi/2v_t$, $b = 1$, $c = v_t/2 - v_p$ and $d = 1$. The PDF of the minimum of $\underline{r_1}$ and $\underline{r_2}$ is found using (see appendix) (A 2):

$$f_{\underline{R}}(\underline{r}) = \int_{\underline{r}}^{\infty} (f_{\underline{R_1 R_2}}(\underline{r}, w) + f_{\underline{R_1 R_2}}(w, \underline{r}))\,dw. \tag{5.5}$$

The joint PDF of $\underline{r}$ and s is $f_{\underline{R}S}(\underline{r}, s) = f_{\underline{R}}(\underline{r}) f_S(s)$ [40], assuming the minimum distance and the strike distance are independent. The probability of capture $P_{\text{CoA}} = E[\hat{C}(\underline{r}, s)]$, where $\hat{C}(\underline{r}, s)$ is an auxiliary function that takes value $C(s)$, if $\underline{r} \leq s$, and 0 otherwise. From (see appendix) (A 3), we have the probability of capture on approach

$$P_{\text{CoA}} = \int_{-\infty}^{\infty} C(s)f_S(s)\left(\int_{-\infty}^{s} f_{\underline{R}}(\underline{r})\,d\underline{r}\right)ds. \tag{5.6}$$

The above equation provides the probability that the prey is captured on a given approach of the predator. Applying this equation to the case-study data yields $P_{\text{CoA}} = 0.07$. As a check, the dynamics given in figure 7 were simulated until the result was invariant to the number of simulations and it was found that P_{CoA} matched the result from (5.6). For each
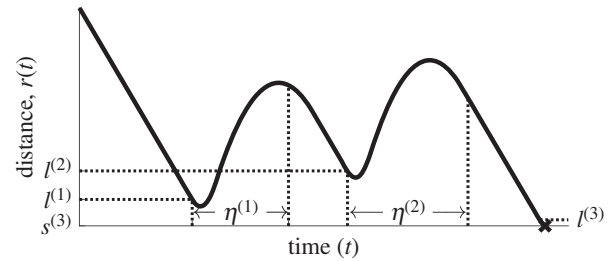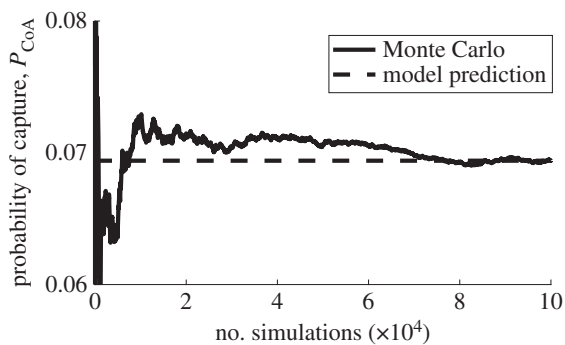

Figure 8. Sample trajectory of simulated dynamics in figure 7 using the zebrafish case-study data and model. The prey begins escape three times before a strike occurs at the black $\times$.

Figure 9. Monte Carlo simulation results of the dynamics in §5. The dashed line indicates the prediction of (5.6).

Figure 10. Probability of suvival $P_{SnA}(1) = 1 - P_{CoA}$ for $n = 1$ approach, as the means of the parameter distributions are varied. (Online version in colour.)

trial in the simulation, $r(t)$ was integrated using a first-order Euler method. To calculate P_{CoA}, the total number of captures was divided by the total number of trials in the simulation. Figure 9 shows the result of the Monte Carlo trials, where 100 000 trials were needed to converge to the output of the single equation (5.6).

Assuming each approach is an independent event, the probability that the prey survives after n approaches is [40]

$$P_{SnA}(n) = (1 - P_{CoA})^n. \tag{5.7}$$

Equation (5.7) in conjunction with (5.6) allows experimentally gathered PDFs of predator–prey parameters to be used to calculate the odds of prey survival after repeated approaches by the predator. Note that as $n \to \infty$, $P_{SnA}(n) \to 0$ and thus the prey are always captured eventually.

Parameter perturbation analysis. Equations (5.5) and (5.6) allow interrogation of experimentally gathered data to find which parameters are most important in the predator–prey interaction. By shifting the mean of the probabilistic parameters (or shifting the values of the deterministic parameters) and recalculating (5.6), the most important parameters to prey survival become readily apparent.

Figure 10 shows the result of the perturbation analysis. Increasing sensing range l and maximum escape speed v_t increases the probability of survival of the prey. However, there is a larger increase seen when the sensing range is increased rather than escape speed. Increasing escape duration η decreases probability of survival, likely because it takes the prey longer to reach its maximum speed (escape duration and maximum speed determine acceleration). Parameter χ, the fraction of the escape time at which the prey reaches its maximum speed, matches the result of varying η almost exactly because both terms determine the prey's acceleration on the first leg of its velocity profile.

When strike distance s is increased, the probability of survival also increases. In this case study, the decrease in probability of capture that results from the condition $\underline{r} \leq s$ is outweighed by the decrease in likelihood of a strike being successful at the increased range (capture probability $C(s)$ is much lower when striking from a farther distance). Decreasing s decreases prey survival only up until a point where the trend reverses. The probability densities interact such that the increased odds of a successful strike at a short distance eventually outweigh the chance that the prey escapes due to sensing the predator before it can strike.

Discussion. Trend-reversing behaviour such as is seen here when strike distance is varied cannot be predicted from the dynamics of the non-deterministic hybrid system
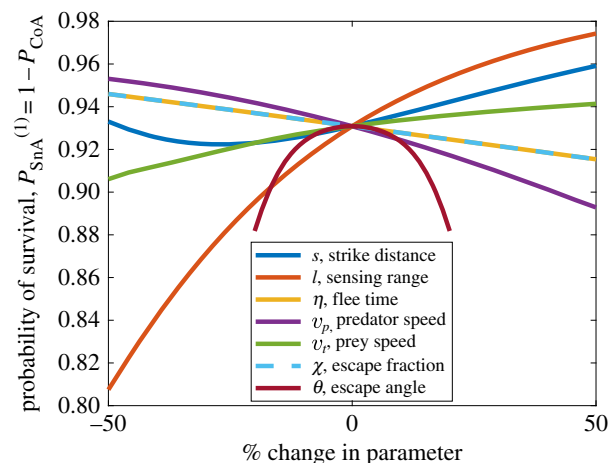
presented in figure 7 alone, as it depends on the particular parameter PDFs. The ability to predict behaviour of this type by combining experimentally fit PDFs with a model of the dynamics is a strength of the data-driven approach. In this case study, sensing range is pivotal to prey survival. Especially, in the negative changes in l, there is a much larger decrease in survivability compared to the other parameters. These results agree with those of a comparable analysis performed by a Monte Carlo simulation [28], but was resolved here analytically.

The PAM method gives something more than agreement with numerical simulations for this case study: it explains *why* sensing range is most important. The derivation of the probability of capture revealed that it is imperative to increase the minimum distance if the prey wishes to survive. The analytical expressions (5.2,5.3) for the minimum distance show that it has a one-to-one correspondence with sensing range. (Compare this observation to the other parameters that enter the expressions multiplied by other factors.) To increase survivorship, natural selection would favour individuals with greater sensing range more so than greater speed. However, to account for additional features such as a requirement of the prey to feed or predators that have difficulty sensing motionless prey, the model used here is insufficient. Special consideration would be needed in that case, which adds complexity to the model formulation.

Figure 10 also includes a curve corresponding to varying escape angle θ from a nominal value of 2π, which corresponds to when the prey flees directly away from the predator. Since our dynamics model is one dimensional, a reasonable approximation to the two-dimensional concept of escape angle is to reduce the effective escape speed to $u_{eff} = u\cos\theta$. We see that in our model any variations away from direct escape result in lower chances of survival, something not seen in [28]. Our choice to represent the pursuit in only the one-dimension r ignores any turning dynamics that may exist in the predators motion, i.e. it is always heading directly towards the prey. This choice neglects the potential tactic of the prey of changing its escape direction unexpectedly after each escape phase, thereby requiring the predator to change its orientation with some associated time delay corresponding to its turning dynamics. Expanding this model to include turning dynamics of the predator and thereby allowing an investigation of the benefit of unpredictability in the prey's escape angle is a suitable topic for ongoing work.

6. Conclusion

This study models the tactical behaviour of predator or prey with a novel combination of analytical mathematics and data-driven variability called PAM. Experimental measurements of kinematic features such as speed and flush distance combined with PAM predicts the outcomes of biological events in ways that experiments or modelling alone cannot. Our first case study showed that the trajectory of a bluefish predator may be predicted with a DPP tactic. Analysis of this tactic revealed no substantial advantage compared to PP, indicating that the small, non-zero values for the pursuit angle may indicate a sensorimotor bias or perhaps a tactical advantage not revealed by the prey species presently considered. The second case study on zebrafish predicted the survivorship of prey using a simple evasion algorithm. Analysis of this model was consistent with previous numerical results showing that sensing range is most important to survival among the behavioural parameters of the prey. In both case studies, PAM demonstrates the utility of a principled approach for understanding tactics in predation.

Beyond predator–prey interactions, the PAM method offers advantages for the modelling of a variety of dynamical systems. These benefits compare well against a Monte Carlo method, which may similarly incorporate measurements but requires numerical simulations to formulate its predictions. Unlike Monte Carlo, the predictions of PAM do not vary with the number of simulations or the tolerances of the numerical solver [49]. PAM scales well with the number of probabilistic variables in the model, whereas the number of Monte Carlo simulations required to formulate a prediction is a multiple of these variables. Models with stochastic processes additionally challenge the capacity of numerical solvers to converge or arrive at an accurate solution [50]. Therefore, the capacity of PAM to formulate predictions through analytical means should become increasingly more apparent for systems of greater complexity.

Authors' contributions. B.A.F. developed the probabilistic analytical modelling technique, applied the technique to the case studies and drafted much of the manuscript. M.J.M. provided biological insight into the study results, participated in planning the structure of the manuscript and drafted much of the introduction, background and discussion sections. D.A.P. conceived of the study, coordinated the study and helped draft the manuscript. All authors gave final approval for publication.

Appendix A

Given random variable $Z = \min(X, Y)$, let us compute $f_Z(z)$. We first state that from the definition of a cumulative distribution function $F_Z(z) = P[\min(X, Y) \leq z]$. The event $\min(X, Y) \leq z$ is true if either $X \leq z$ or $Y \leq z$. In set notation,

$$
\begin{aligned}
F_Z(z) &= P[\min(X, Y) \leq z] \\
&= P[X \leq z \cup Y \leq z] \\
&= P[X \leq z] + P[Y \leq z] - P[X \leq z \cap Y \leq z] \\
&= F_X(z) + F_Y(z) - F_{XY}(z, z),
\end{aligned}
\tag{A 1}
$$

where the third line is a direct application of the inclusion–exclusion principle, which states that, for two events A and B, $P[A \cup B] = P[A] + P[B] - P[A \cap B]$ [40]. To find the PDF from the CDF (A 1), we take the derivative with respect to z, i.e.

$$
\begin{aligned}
f_Z(z) &= \frac{\mathrm{d}F_z(z)}{\mathrm{d}z} = f_X(z) + f_Y(z) - \frac{\mathrm{d}}{\mathrm{d}z} F_{XY}(z, z) \\
&= f_X(z) + f_Y(z) - \int_{-\infty}^{z} (f_{XY}(z, w) + f_{XY}(w, z)) \, \mathrm{d}w \\
&= \int_{-\infty}^{\infty} f_{XY}(z, w) \, \mathrm{d}w + \int_{-\infty}^{\infty} f_{XY}(w, z) \, \mathrm{d}w \\
&\quad - \int_{-\infty}^{z} (f_{XY}(z, w) + f_{XY}(w, z)) \, \mathrm{d}w \\
&= \int_{z}^{\infty} (f_{XY}(z, w) + f_{XY}(w, z)) \, \mathrm{d}w.
\end{aligned}
\tag{A 2}
$$

For independent random variables X and Y, the expected value of

$$
h(X, Y) = \begin{cases} g(Y) & \text{if } X \leq Y, \\ 0 & \text{otherwise} \end{cases}
$$

is

$$
\begin{aligned}
E[h(X, Y)] &= \iint_{-\infty\,-\infty}^{\infty\,\infty} h(x, y) f_{XY}(x, y) \, \mathrm{d}x \, \mathrm{d}y \\
&= \iint_{-\infty\,-\infty}^{\infty\,\infty} h(x, y) f_X(x) f_Y(y) \, \mathrm{d}x \, \mathrm{d}y \\
&= \begin{cases} \iint_{-\infty\,-\infty}^{\infty\,\infty} g(y) f_X(x) f_Y(y) \, \mathrm{d}x \, \mathrm{d}y & \text{if } X \leq Y \\ 0 & \text{otherwise} \end{cases} \\
&= \iint_{-\infty\,-\infty}^{\infty\,y} g(y) f_X(x) f_Y(y) \, \mathrm{d}x \, \mathrm{d}y \\
&= \int_{-\infty}^{\infty} g(y) f_Y(y) \left(\int_{-\infty}^{y} f_X(x) \, \mathrm{d}x \right) \mathrm{d}y.
\end{aligned}
\tag{A 3}
$$

References

1. Hamilton WD. 1971 Geometry for the selfish herd. *J. Theor. Biol.* **31**, 295–311. (doi:10.1016/0022-5193(71)90189-5)

2. Bakolas E, Tsiotras P. 2010 Optimal pursuit of moving targets using dynamic Voronoi diagrams. In *Proc. IEEE Conf. on Decision and Control, IEEE*, pp. 7431–7436. (doi:10.1109/CDC.2010.5717963)

3. Scott W, Leonard NE. 2014 Dynamics of pursuit and evasion in a heterogeneous herd. In *Proc. IEEE Conf. on Decision and Control*, pp. 2920–2925. (doi:10.1109/CDC.2014.7039838)

4. Kim T-H, Sugie T. 2007 Cooperative control for target-capturing task based on a cyclic pursuit strategy. *Automatica* **43**, 1426–1431. (doi:10.1016/j.automatica.2007.01.018)

5. Shishika D, Paley DA. 2017 Mosquito-inspired swarming for decentralized pursuit with autonomous vehicles. In *American Control Conf., IEEE*, pp. 923–929. (doi:10.23919/ACC.2017.7963071)1

6. Shneydor NA. 1998 *Missile guidance and pursuit: kinematics, dynamics, and control.* Chichester, UK: Horwood.

7. Nahin PJ. 2012 *Chases and escapes: the mathematics of pursuit and evasion*. Princeton, NJ: Princeton University Press.

8. Wei E, Justh EW, Krishnaprasad P. 2009 Pursuit and an evolutionary game. *Proc. R. Soc. A* **465**, 1539–1559. (doi:10.1098/rspa.2008.0480)

9. Isaacs R. 1965 *Differential games*. New York, NY: John Wiley and Sons.

10. Weihs D, Webb P. 1984 Optimal avoidance and evasion tactics in predator–prey interactions. *J. Theor. Biol.* **106**, 189–206. (doi:10.1016/0022-5193(84)90019-5)

11. Soto A, Stewart WJ, McHenry MJ. 2015 When optimal strategy matters to prey fish. *Integr. Comp. Biol.* **55**, 110–120. (doi:10.1093/icb/icv027)

12. Domenici P, Batty R. 1994 Escape manoeuvres of schooling *Clupea harengus*. *J. Fish. Biol.* **45**, 97–110. (doi:10.1111/j.1095-8649.1994.tb01086.x)

13. Domenici P, Blake RW. 1991 The kinematics and performance of the escape response in the angelfish (*Pterophyllum eimekei*). *J. Exp. Biol.* **156**, 187–205.

14. Blaxter JHS, Fuiman LA. 1990 The role of the sensory systems of herring larvae in evading predatory fishes. *J. Mar. Biol. Assoc. UK* **70**, 413–427. (doi:10.1017/S0025315400035505)

15. Eaton RC, Didomenico R, Nissanov J. 1988 Flexible body dynamics of the goldfish C-start: implications for reticulospinal command mechanisms. *J. Neurosci.* **8**, 2758–2768. (doi:10.1523/jneurosci.08-08-02758.1988)

16. Stewart W, Nair A, Jiang H, McHenry M. 2014 Prey fish escape by sensing the bow wave of a predator. *J. Exp. Biol.* **217**, 4328–4336. (doi:10.1242/jeb.111773)

17. Vabø R, Nøttestad L. 1997 An individual based model of fish school reactions: predicting antipredator behaviour as observed in nature. *Fish. Oceanogr.* **6**, 155–171. (doi:10.1046/j.1365-2419.1997.00037.x)

18. Calovi DS, Lopez U, Schuhmacher P, Chaté H, Sire C, Theraulaz G. 2015 Collective response to perturbations in a data-driven fish school model. *J. R. Soc. Interface* **12**, 20141362. (doi:10.1098/rsif.2014.1362)

19. Willman W. 1969 Formal solutions for a class of stochastic pursuit-evasion games. *IEEE Trans. Autom. Control* **14**, 504–509. (doi:10.1109/tac.1969.1099249)

20. James A, Baxter PD, Pitchford JW. 2005 Modelling predation as a capped rate stochastic process, with applications to fish recruitment. *J. R. Soc. Interface* **2**, 477–487. (doi:10.1098/rsif.2005.0063)

21. Mwaffo V, Anderson RP, Butail S, Porfiri M. 2015 A jump persistent turning walker to model zebrafish locomotion. *J. R. Soc. Interface* **12**, 20140884. (doi:10.1098/rsif.2014.0884)

22. Kane EA, Higham TE. 2014 Modelled three-dimensional suction accuracy predicts prey capture success in three species of centrarchid fishes. *J. R. Soc. Interface* **11**, 20140223. (doi:10.1098/rsif.2014.0223)

23. Boets P, Lock K, Messiaen M, Goethals PL. 2010 Combining data-driven methods and lab studies to analyse the ecology of *Dikerogammarus villosus*. *Ecol. Inform.* **5**, 133–139. (doi:10.1016/j.ecoinf.2009.12.005)

24. Dattner I, Miller E, Petrenko M, Kadouri DE, Jurkevitch E, Huppert A. 2017 Modelling and parameter inference of predator–prey dynamics in heterogeneous environments using the direct integral approach. *J. R. Soc. Interface* **14**, 20160525. (doi:10.1098/rsif.2016.0525)

25. Chauvet E, Paullet JE, Previte JP, Walls Z. 2002 A Lotka–Volterra three-species food chain. *Math. Mag.* **75**, 243–255. (doi:10.2307/3219158)

26. Leslie P, Gower J. 1960 The properties of a stochastic model for the predator–prey type of interaction between two species. *Biometrika* **47**, 219–234. (doi:10.2307/2333294)

27. Oremland M, Laubenbacher R. 2015 Optimal harvesting for a predator–prey agent-based model using difference equations. *Bull. Math. Biol.* **77**, 434–459. (doi:10.1007/s11538-014-0060-6)

28. Nair A, Nguyen C, McHenry M. 2017 A faster escape does not enhance survival in zebrafish larvae. *Proc. R. Soc. B* **284**, 20170359. (doi:10.1098/rspb.2017.0359)

29. McHenry M, Johansen J, Soto A, Free B, Paley D, Liao J. Submitted. The pursuit strategy of predatory bluefish (*Pomatomus saltatrix*), *Proc. R. Soc. Lond. B*.

30. Lanchester BS, Mark RF. 1975 Pursuit and prediction in the tracking of moving food by a teleost fish (*Acanthaluteres spilomelanurus*). *J. Exp. Biol.* **63**, 627–645.

31. Mizutani A, Chahl JS, Srinivasan MV. 2003 Insect behaviour: motion camouflage in dragonflies. *Nature* **423**, 604–604. (doi:10.1038/423604a)

32. Ghose K, Horiuchi TK, Krishnaprasad P, Moss CF. 2006 Echolocating bats use a nearly time-optimal strategy to intercept prey. *PLoS Biol.* **4**, e108. (doi:10.1371/journal.pbio.0040108)

33. Guelman M. 1971 A qualitative study of proportional navigation. *IEEE Trans. Aerosp. Electron. Syst.* **AES-7**, 637–643. (doi:10.1109/taes.1971.310406)

34. Shima T. 2007 Deviated velocity pursuit. In *Proc. of the AIAA Guidance, Navigation, and Control Conf., Hilton Head, SC*. (doi:10.2514/6.2007-6782)

35. Olberg R, Worthington A, Venator K. 2000 Prey pursuit and interception in dragonflies. *J. Comp. Physiol. A* **186**, 155–162. (doi:10.1007/s003590050015)

36. Shaffer DM, Krauchunas SM, Eddy M, McBeath MK. 2004 How dogs navigate to catch frisbees. *Psychol. Sci.* **15**, 437–441. (doi:10.1111/j.0956-7976.2004.00698.x)

37. Fajen BR, Warren WH. 2004 Visual guidance of intercepting a moving target on foot. *Perception* **33**, 689–715. (doi:10.1068/p5236)

38. Kane SA, Zamani M. 2014 Falcons pursue prey using visual motion cues: new perspectives from animal-borne cameras. *J. Exp. Biol.* **217**, 225–234. (doi:10.1242/jeb.092403)

39. Justh EW, Krishnaprasad P. 2006 Steering laws for motion camouflage. *Proc. R. Soc. A* **462**, 3629–3643. (doi:10.1098/rspa.2006.1742)

40. Stark H, Woods JW. 1986 *Probability, random processes, and estimation theory for engineers*. Upper Saddle River, NJ: Prentice Hall.

41. Bishop CM. 2006 *Pattern recognition and machine learning*. Berlin, Germany: Springer.

42. Duin R, Juszczak P, Paclik P, Pekalska E, De Ridder D., Tax D, Verzakov S. 2000 A Matlab toolbox for pattern recognition. *PRTools version* **3**, 109–111.

43. Stewart W, Cardenas G, McHenry M. 2013 Zebrafish larvae evade predators by sensing water flow. *J. Exp. Biol.* **216**, 388–398. (doi:10.1242/jeb.072751)

44. Lygeros J. 2004 Lecture notes on hybrid systems. In *Notes for an ENSIETA Workshop*. See https://fenix.tecnico.ulisboa.pt/downloadFile/3779579688470/lygeros.pdf.

45. Goebel R, SanFelice RG, Teel AR. 2009 Hybrid dynamical systems. *IEEE Control Syst. Mag.* **29**, 28–93. (doi:10.23943/princeton/9780691153896.001.0001)

46. Hu J, Lygeros J, Sastry S. 2000 Towards a theory of stochastic hybrid systems. In *Hybrid systems: computation and control*, pp. 160–173. Berlin: Springer. (doi:10.1007/3-540-46430-1_16)

47. Isaacs R. 1965 *Differential games: a mathematical theory with applications to warfare and pursuit, control and optimization*. New York, NY: Dover.

48. Grimmett G, Stirzaker D. 2001 *Probability and random processes*. Oxford, UK: Oxford University Press.

49. Driels MR, Shin YS. 2004 Determining the number of iterations for Monte Carlo simulations of weapon effectiveness. Technical Report, Naval Postgraduate School, Dept. of Mechanical & Astronautical Engineering.

50. Kloeden PE, Platen E, Schurz H. 2012 *Numerical solution of SDE through computer experiments*. Springer Science & Business Media. (doi:10.2307/1269175)