Non-deterministic Predator-Prey Model with Accelerating Prey

Brian A. Free, Matthew J. McHenry, and Derek A. Paley

***Abstract*— This paper presents a data-driven, non-deterministic model of the dynamics of predator-prey interactions where the prey accelerates to a speed faster than the predator speed. The method proposed in this work predicts the probability of prey survival after a given number of approaches. The work presented here makes no assumptions about the form of the probability density function (PDF) of model parameters such as escape time, sensing range, strike distance, and strike success rate. It may therefore use empirical PDFs, i.e., those collected in biological experiments, for calculating the probability of capture. This allows for an investigation of parameters that are the most important to prey survival. A case study of the predation of larval zebrafish by adult zebrafish demonstrates the proposed technique.**

I. INTRODUCTION

The interaction between predator and prey is of interest to biological and engineering research [1]. The prey's survival may depend on features such as sensing range and escape speed, and improving these features is of evolutionary significance. It is therefore important to be able to identify the crucial factors that determine prey survival.

This manuscript presents a non-deterministic hybrid system model of predator-prey interaction. We provide a formal method to calculate the probability of prey capture on a single approach from a predator and the probability of survival after multiple approaches. Measured probability density functions (PDFs) for the predator parameters (such as strike range, maximum speed, and the success rate of strikes) and the prey parameters (such as sensing range, maximum speed, and escape time) are used to calculate the prey survival probability. Additionally, altering the distributions for these parameters to perform a sensitivity analysis identifies the most critical components to survival.

In many predator-prey relationships, the predator is faster but less agile than the prey [2]. The model presented here considers predator-prey interactions where the prey escapes by accelerating to a speed that is faster than the predator speed. The model includes the possibility of many repeated approaches by the predator until the prey is captured.

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Understanding the dynamics of predator-prey interaction is a rich field of study. Various types of pursuit and evasion strategies for predation have been modeled and examined at length [3]–[5]. The dynamics of a single predator pursuing many prey (i.e., a herd or school) have been extensively examined and modeled [6]–[8], as well as swarming behavior with one target and many pursuers [9], [10].

Predator-prey relationships that include randomness also have a strong foundation in research. An individual-based dynamic model for schooling fish that includes stochastic elements predicts behavioral responses to a predator [11]. A predator-prey model that includes stochastic process noise in the dynamics of the players as well as their measurements provides formal solutions for the dynamics [12]. Leslie and Gower studied the populations dynamics of a predator-prey system with stochastic components to the birth and death rate of the species [13].

To relate individual player dynamics to population sizes, Oremland and Laubenbacher developed a method to generalize the local predator-prey interactions to the population dynamics of each species [14]. In practical research on a specific species, data-driven modeling methods combined with experimental work identify key features of predation by the exotic shrimp species *Dikerogammarus villosus* [15]. In contrast to the work herein, where the prey is faster than the predator, Li examined the case where the predator is faster than a more agile prey [2]. To the authors' knowledge, there exists no prior work that develops a non-deterministic hybrid system model of predator-prey interaction permitting data-driven analysis to determine the key factors of prey survival.

To calculate the probability of capture on the approach of a predator, a one-dimensional hybrid system model of the dynamics is presented. The continuous part of the hybrid system describes the approach of the predator and the escape behavior of the prey, whereas the discrete part handles the switching of parameters between repeated approaches. We identify the conditions necessary for prey capture and apply tools from probability theory to derive an equation for the probability of capture on approach. To find which parameters in the model have the most influence on prey survival, we present two techniques. The first relies on altering the experimentally determined probability densities, whereas the second technique uses the partial derivatives of the minimum distance between predator and prey with respect to the expected values of the parameters.

The contributions of this paper are (1) a one-dimensional, non-deterministic hybrid system model of the dynamics of the predator-prey interaction; (2) a non-dimensional analysis of the assumption that the minimum distance between predator and prey occurs before the prey has reached its maximum speed; (3) a data-driven equation accepting empirical probability density functions of predator and prey parameters to calculate the probability of prey capture; and (4) two techniques to interrogate experimentally gathered probabilities to identify model parameters most important to prey survival. These techniques allow researchers to investigate key factors of survival by observing predator-prey interactions, and may have implications for pursuit behavior in robotic systems. The techniques developed here are demonstrated on a case study of the predation of larval zebrafish by adult zebrafish. The one-dimensional predator-prey model here is a precursor to a more general pursuit model in two or three dimensions.

The paper proceeds as follows. Section II provides technical background in probability theory and hybrid systems, and describes the case-study data used throughout to demonstrate the use of the model. Section III presents the dynamical model used in this work and a non-dimensional analysis of the key assumption that the minimum distance between predator and prey occurs before the prey has reached its maximum speed. Section IV derives the equation used to calculate the probability of capture on approach by the predator. Section V presents two techniques that investigate predator/prey parameters to identify which parameters in the model are most important to prey survival and Section VI summarizes the results and describes ongoing work.

II. Background

A. Probability Theory and Hybrid Systems

Developing the techniques used in this manuscript requires tools from probability theory [16]. The probability that a random variable X has value less than x is described by the cumulative distribution function $F_X(x) = P(X \leq x)$. The probability density function 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 probability density functions to a data set [17], [18].

The expected value of a random variable X with probability density $f_X(x)$ is [16]

$$E[X] = \int_{-\infty}^{\infty} x f_X(x) dx. \tag{1}$$

The expected value of a function $Y = h(X)$ of random variable X with probability density $f_X(x)$ is [16]

$$E[Y] = \int_{-\infty}^{\infty} h(x) f_X(x) dx. \tag{2}$$

The probability that random variable X is less than random variable Y is [16]

$$P(X \leq Y) = \iint_{-\infty\,-\infty}^{\infty\;\;y} f_{XY}(x,y) dx dy, \tag{3}$$

where $f_{XY}(x,y)$ is the joint probability density function of X and Y. If X and Y are independent random variables, then [16]

$$f_{XY}(x,y) = f_X(x) f_Y(y), \tag{4}$$

otherwise the joint probability density must account for cross-correlation between the two random variables. The probability density function for the random variable Z given by $Z = c_1 X + c_2 Y$, where c_1 and c_2 are known scalar values, is [16]

$$f_Z(z) = \frac{1}{\mid c_1 \mid} \int_{-\infty}^{\infty} f_X\left(\frac{1}{c_1} z - \frac{c_2}{c_1} y\right) f_Y(y) dy. \tag{5}$$

If two events A and B are independent, then the probability of both A and B occurring at the same time is [16]

$$P(A \cap B) = P(A)P(B). \tag{6}$$

Lemma 1: The expected value of a function

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

of independent random variables X and Y with probability density functions $f_X(y)$ and $f_Y(y)$ is

$$E[h(X,Y)] = \int_{-\infty}^{\infty} g(y) f_Y(y) \left(\int_{-\infty}^{y} f_X(x) dx \right) dy.$$

Lemma 1 can be proven by using the bivariate extension of (2), the independence of X and Y with (4), and (3). It is used in Section IV to determine the probability of capture.

The dynamic model of the predator-prey interaction presented in Section III is an example of a hybrid system. A hybrid system is a dynamical system that has a combination of continuous- and discrete-time behavior [19], [20]. 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 [21]. We refer to the model developed herein as a non-deterministic hybrid system rather than a stochastic hybrid system to avoid the connotation of explicit time-dependence of the random variables. Instead the parameters are drawn randomly from the corresponding probability distribution once per approach; each predator-prey interaction can encompass multiple approaches.

B. Case study

Although the model proposed in this paper is general to a variety of predator-prey interactions, it was initially developed to investigate a case study of zebrafish. Zebrafish adults prey on larvae of the same species under laboratory conditions [22]. This allows the kinematics of both predator and prey to be measured with high-speed video over the entirety of predatory strikes, until the prey is ingested [23]. Such experiments have established that the predator targets the prey with a pure pursuit strategy, such that its heading is directed towards the instantaneous position of the prey. The larval prey are generally stationary during the predator's approach, until initiating an escape response when the predator is in close proximity [24]. The predator approaches the prey at a constant speed that is well below the prey's maximum escape speed. Within one second of initiating an escape, the prey ceases swimming and may

Probabilistic Parameters	s	Strike distance of predator
	l	Sensing distance of prey
	η	Escape duration of prey
Deterministic Parameters	U	Maximum predator speed
	u	Maximum prey speed
	χ	Fraction of η when u is reached
Deterministic Functions	$C(s)$	Strike probability of success as a function of strike distance

TABLE I: Parameters of the model. Probabilistic parameters have probability density functions $f_S(s)$, $f_L(l)$, and $f_H(\eta)$.

be stimulated to escape again when approached by the predator. These interactions repeat for as many as twenty approaches in experiments performed in a relatively small aquarium [23]. The dynamics of predator-prey interactions in zebrafish is well-characterized by iterating a model of a single interaction.

Throughout this manuscript, the developed techniques are applied to the zebrafish case study. The parameters presented in Section III were determined experimentally in a previous work [23] by studying the predation of larval zebrafish (*Danio rerio*) by adult and juvenile zebrafish. A two-dimensional numerical model was described in [23] to calculate the probability of capture through Monte Carlo simulations. Here we provide an alternate means to examine pursuit systems, where the probability of capture can be determined mathematically as a function of the probability densities pertaining to the system parameters.

III. Hybrid Pursuit Model

This section presents a one-dimensional model of pure pursuit predator-prey interactions. We examine a one-dimensional model in order to develop the data-driven techniques used to analyze dynamical system with probabilistic parameters. Ongoing work extends to planar pursuit, though as will be shown, the one-dimensional model presented here yields the same results as the two-dimensional Monte Carlo style methods used in the original case study [23]. Among pursuit strategies [3]–[5], pure pursuit 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 escape if $r(t)$ is less than its sensing range l. The prey escapes for η seconds, reaching its maximum speed u 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 may be experimentally determined. Table I summarizes the parameters used in the model.

Assume that the predator reaches is maximum speed U 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 Fig. 1. 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 [23].

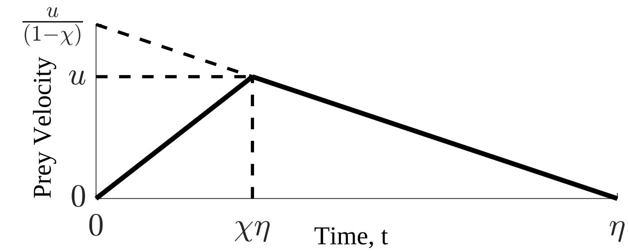

Fig. 1: Prey velocity profile after detecting the predator. The prey escape duration is η; it reaches its maximum speed at fraction χ of the escape duration.

Figure 2 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, every time a_n increments, 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 3 shows a sample trajectory of the dynamics using case-study data.

Critical to our analysis is finding the minimum distance $\underline{r}^{(n)}$ between the predator and prey. When it is clear from context, the superscript (n) is omitted, e.g., from $\underline{r}^{(n)}$. Assume that the minimum distance occurs during the first leg of the escape phase, when $0 < t^{(n)} < \chi\eta^{(n)}$, rather than at the end of the escape cycle, when $t^{(n)} = \eta^{(n)}$. Proposition 1 states when it is valid to make this assumption.

Proposition 1: Let $U^* = U/u$ denote the ratio of the predator speed and the maximum prey speed. If the minimum distance $\underline{r}$ occurs while the prey is still accelerating, then $U^* \leq U^*_{\text{crit}}$, where

$$U^*_{\text{crit}} = \frac{1-\sqrt{1-\chi}}{\chi}. \tag{7}$$

Proof: Non-dimensionalize the dynamics of a single approach using

$$t^* = \frac{t^{(n)}}{\eta^{(n)}}, \quad r^* = \frac{r}{l^{(n)}}, \quad U^* = \frac{U}{u}, \text{ and } u^* = \frac{u}{u} = 1.$$

Only consider the period of time that the prey is escaping (because the minimum distance never occurs outside of this period, so long as the prey has non-zero sensing range). The non-dimensional dynamics are

$$\dot{r}^*(t^*) = \begin{cases} -U^* + \frac{1}{\chi}t^* & \text{for } 0 < t^* < \chi \\ -U^* + \frac{1}{1-\chi} - \frac{1}{(1-\chi)}t^* & \text{for } \chi < t^* < 1. \end{cases} \tag{8}$$

Integrating the dynamics and letting r_1^* and r_2^* be the distance

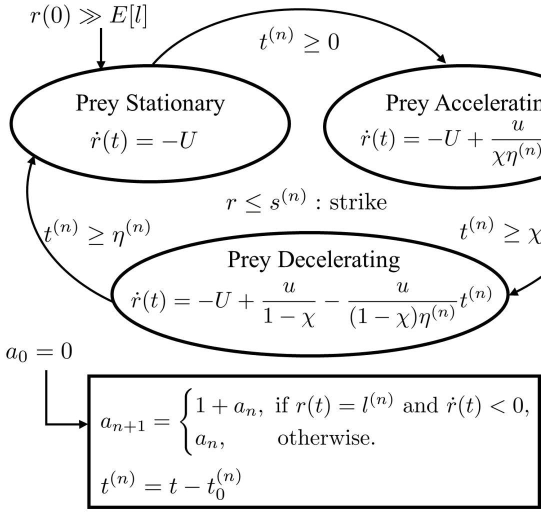

Fig. 2: Non-deterministic hybrid system model of predator-prey interaction. The box represents the discrete dynamics and the ellipses represent continuous dynamics. Probabilistic variables are redrawn from their respective PDFs each time the approach number a_n is incremented.

on the first and second legs, respectively, yields

$$r_1^*(t^*) = -U^* t^* + \frac{1}{2\chi} t^{*2} + 1$$
$$r_2^*(t^*) = \left(-U^* + \frac{1}{1-\chi}\right) t^* - \frac{1}{2(1-\chi)} t^{*2} + \frac{3\chi - 2}{2(\chi - 1)},$$

where the constants of integration were found from the boundary conditions $r_1^*(0) = 1$ and $r_1^*(\chi) = r_2^*(\chi)$. The minimum $\underline{r}^*$ will either occur on the first leg at $t^* = U^*\chi$ or at the end of the second leg. So the condition on U^*_{crit} becomes $r_1^*(U^*_{\text{crit}}\chi) = r_2^*(1)$, which implies (7). ■

Equation (7) defines an upper bound on the ratio of predator speed to prey speed as a function of $\chi \in [0, 1]$. The extremes of this function are of interest. For $\chi = 0$, meaning the prey reaches its maximum speed instantaneously, the critical ratio is

$$\lim_{\chi \to 0} U^*_{\text{crit}} = \frac{1}{2},$$

using L'Hospital's Rule [25]. For $\chi = 1$, meaning the prey reaches its maximum speed at the end of the escape period, $U^*_{\text{crit}} = 1$. Therefore, in the extremes of χ, the results below are valid for when the prey speed is greater than twice the speed of the predator ($\chi = 0$) or when the prey and predator speeds are equal ($\chi = 1$).

Figure 4 shows three trajectories: one where Prop. 1 is valid, the limiting case of Prop. 1, and one where Prop. 1 does not hold. For the case-study data, $U^*_{\text{crit}} = 0.53$; the techniques developed in this paper require $U \leq 0.53\, u$, which is met with $U^* = 0.35$ [23].

This analysis is independent of the predator and prey species, allowing the techniques herein to be applied generally to any predator/prey pair demonstrating pure pursuit with an escape response. So long as the above condition on the ratio of the predator and prey maximum speeds is met, the assumption that $\underline{r}$ occurs before the prey has reached its

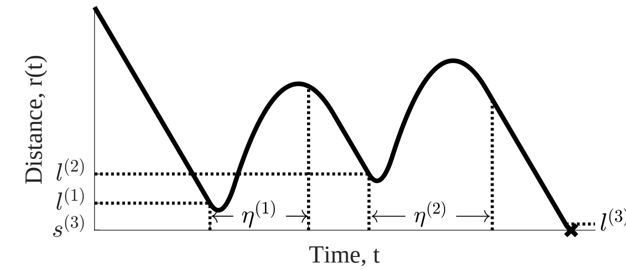

Fig. 3: Sample trajectory of dynamics in Fig. 2 using the zebrafish case-study data. The prey begins escape three times before a strike occurs at the black $\times$.

maximum speed is valid.

IV. Analysis of Survival Probability

With the goal to find the minimum distance $\underline{r}$ on a single approach, Prop. 1 allows us to consider only the portion of the dynamics before the prey has reached its maximum speed. Thus, from Fig. 2, we have

$$\dot{r}(t) = -U + \frac{u}{\chi\eta} t, \qquad (9)$$
$$r(0) = l,$$

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, the distance between predator and prey is

$$r(t) = l - Ut + \frac{1}{2}\frac{u}{\chi\eta} t^2.$$

Setting (9) equal to zero, $\underline{r}$ achieves a minimum at $\underline{t} = U(\chi\eta/u)$. Thus we have

$$\underline{r}(\eta, l) = -\frac{U^2\chi}{2u}\eta + l, \qquad (10)$$

which is a linear combination of two random variables: η, the prey escape time, and l, the prey sensing distance.

Equation (5) allows us to calculate the equivalent probability density function of $\underline{r}$ from $f_H(\eta)$ and $f_L(l)$. With $c_1 = -U^2\chi/2u$ and $c_2 = 1$, the PDF for $\underline{r}$ is

$$f_{\underline{R}}(\underline{r}) = \frac{2u}{U^2\chi} \int_{-\infty}^{\infty} f_\eta \left(-\frac{2u}{U^2\chi}\underline{r} + \frac{2u}{U^2\chi} l \right) f_L(l) dl. \qquad (11)$$

The joint probability density function of $\underline{r}$ and s is $f_{\underline{R}S}(\underline{r}, s) = f_{\underline{R}}(\underline{r}) f_S(s)$ from (4), assuming the minimum distance and the strike distance are independent.

For the prey to be captured, two conditions must be met. First, the minimum distance must be less than the strike distance. If $\underline{r}$ is not less than s, then no other point on the trajectory will be either. 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. Thus for the predator-prey interaction described by the dynamics in Fig. 2, the

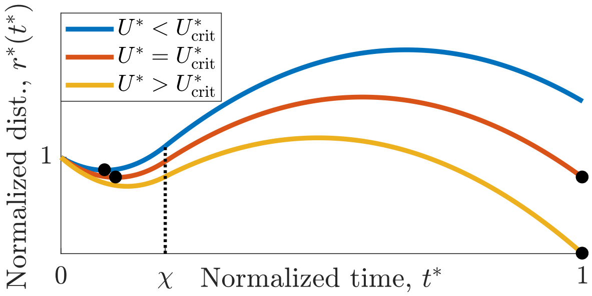

Fig. 4: Three trajectories for the non-dimensional dynamics given in (8). The black circles indicate the minima of each trajectory on this interval.

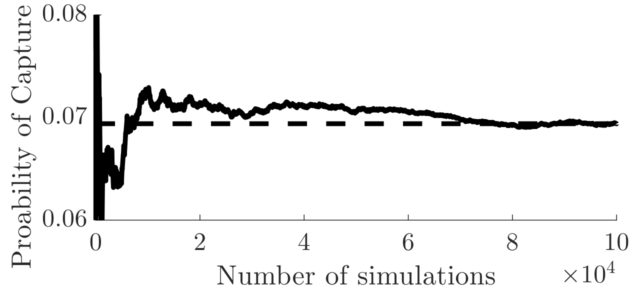

Fig. 5: Monte Carlo simulation results of the dynamics in Section III. The dashed line indicates the prediction of Theorem 1.

probability of capture on approach is

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

We use this reasoning in Theorem 1 below, which is a direct consequence of Lemma 1.

Theorem 1: We extend the definition of $C(s)$ to an auxiliary function $\hat{C}(\underline{r}, s)$ that takes value $C(s)$, if $\underline{r} \leq s$, and 0, otherwise. Then $P_{\text{CoA}} = E[\hat{C}(\underline{r}, s)]$ and, from Lemma 1, we have the probability of capture on approach

$$P_{\text{CoA}} = \int_{-\infty}^{\infty} C(s) f_S(s) \left(\int_{-\infty}^{s} f_{\underline{R}}(\underline{r}) d\underline{r} \right) ds. \tag{12}$$

Theorem 1 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 Fig. 2 were simulated until the result was invariant to the number of simulations and it was found that P_{CoA} matched the result from Theorem 1. For each 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 5 shows the result of the Monte Carlo trials, where 100,000 trials were needed to converge to the output of the single equation (12).

Corollary 1.1: Assuming each approach is an independent event with (6), the probability that the prey survives after n approaches is

$$P_{\text{SnA}}(n) = (1 - P_{\text{CoA}})^n. \tag{13}$$

Equation (13) in conjunction with (12) 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 $n \to \infty$, $P_{\text{SnA}}(n) \to 0$ and thus the prey are always eventually captured.

V. Parameter Perturbation Analysis

Equations (11) and (12) 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 (12) the most important parameters to prey survival become readily apparent. Here we apply this technique to the data from the zebrafish case study [23], which used log-normal probability densities. A change in the log-normal mean adjusts the expected value of the parameter given by (1) to the desired percent-change relative to the nominal value.

Figure 6 shows the result of the perturbation analysis. Increasing sensing range l and maximum escape speed u increases the probability of survival of the prey. However, there is a larger increase seen when 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. Parameter χ, the fraction of the escape time when 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 further 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 such a short distance eventually outweigh the chance that the prey escapes due to sensing the predator before it can strike.

Trend-reversing behavior such as is seen here when strike distance is varied cannot be predicted from the dynamics of the non-deterministic hybrid system presented in Fig. 2, as it depends on the particular parameter PDFs. The ability to predict behavior of this type 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 [23].

Next we suggest a second method to discover which parameters are most important to survival. As seen in Section IV the minimum distance between predator and prey is of key importance to determining the survival of the prey. Particularly, a larger $\underline{r}$ increases the probability of survival of the prey, as shown in (12), where as $\underline{r}$ increases the term in the parentheses decreases. This decrease in P_{CoA} leads to a increase in survivability according to (13). We thus look at the partial derivatives of (10) to see the impact on

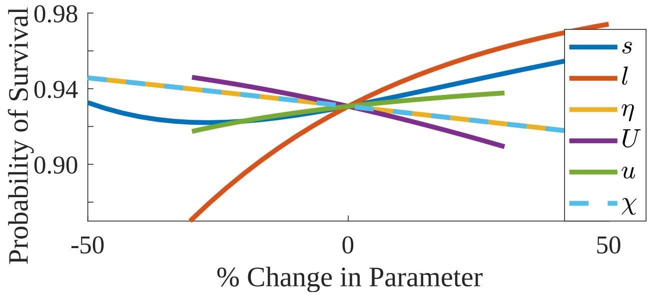

Fig. 6: Probability of suvival P_{SnA} for $n = 1$ approach, as the means of the parameter distributions are varied. Sensing range l is most important to prey survival in this case.

survivability:

$$\frac{\partial \underline{r}}{\partial l} = 1, \qquad \frac{\partial \underline{r}}{\partial \eta} = -\frac{U^2 \chi}{2u} = -0.0049,$$

$$\frac{\partial \underline{r}}{\partial U} = -\frac{U \chi \eta}{u} = -0.0210, \qquad \frac{\partial \underline{r}}{\partial u} = \frac{U^2 \chi \eta}{2u^2} = 0.0036,$$

and $\frac{\partial \underline{r}}{\partial \chi} = -\frac{U^2 \eta}{2u} = -0.0073.$

The values above were calculated from expected values (1) from the case-study data [23]. If increasing $\underline{r}$ improves survivability as suggested above, these partial derivatives qualitatively agree with the perturbation analysis shown in Fig. 6. Lacking from this second technique is a way to determine the effect of changing strike distance s. To examine this parameter the full analysis as shown in Fig. 6 is required.

VI. Conclusion

This paper describes a data-driven, non-deterministic hybrid model for predator-prey interaction and a method to calculate the probability of prey survival. We present a one-dimensional dynamics model and determine its key features to calculate the probability of survival using empirical probability densities of the parameters in the predator-prey interaction. By non-dimensionalizing the dynamics, we provide a necessary condition for the key assumption that the minimum distance between predator and prey occurs before the prey reaches its max speed. A proposed technique to interrogate the experimental data determines the most important parameters for prey survival. The results of applying these techniques to a case study of the predation of larval zebrafish by adult zebrafish agree with prior models and experimental results demonstrating the strategic importance of early predator detection by the prey [1], [23].

Though this worked was developed with the case study in mind, it is general to any predator/prey interaction where the predator exhibits pure pursuit, the prey exhibits an escape response, and the prey achieves a higher maximum speed than the predator.

In ongoing work, we seek to relax the assumption that the minimum distance is achieved before the prey reaches its max speed. Additionally, we plan to include prey and predator maximum speeds as random rather than deterministic variables. The techniques developed in this paper are also being extended to a two-dimensional model inspired by a case study involving predation by bluefish.

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