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Survival depends critically on predator detection in zebrafish larvae

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Abstract

Predation is a fundamental interaction between animals, yet it is largely unclear how prey survive encounters with predators. Using experiments and game modeling, we examined the relative contributions of sensing and locomotion to larval zebrafish when they escape older fish of the same species. High-speed 3D kinematic measurements of interactions between an individual prey when encountering a predator were used to establish the probability distributions of behavioral parameters for both fish. These measurements provided the basis for a game model that simulated the trajectories of predator and prey. The model was verified by having it replicate the frequency distribution of the number of strikes that prey survived. We then conducted a sensitivity analysis to determine which parameters had the greatest influence on prey survival. This analysis found that escape direction and the predator's speed and strike distance has negligible effects on prey survival. Survival instead depends on the response distance and escape speed of prey. For example, prey are more than half as likely to survive if they respond at half the distance of what was observed experimentally. Therefore, strategy in piscivorous interactions depends critically on the ability of prey to detect predators at a distance. This finding informs our understanding for the sensory ecology of a broad diversity of fishes and may indicate a general dynamic in predator-prey interactions.

1. Introduction

Predator-prey interactions offer a context for understanding the biomechanics and neurophysiology of animals. It is commonly argued that the survival of evasive prey and the success of predators depend on fast or highly maneuverable locomotion [1–3]. The rate and force of predatory strikes are similarly considered important factors [4,5], as is the ability of prey to sense an approaching predator at great distance [6,7]. However, it is not clear how these factors compare in their strategic importance to prey survival and it is consequently unknown what traits distinguish successful predators and prey. The aim of the present study was to determine the variables that are most important in determining the survival of a fish when it becomes the prey of a larger fish.

Understanding the dynamics of predators and prey is challenged by the interdependency of both animal's actions. Any motion by a prey may (or may not) be in response to the predator, which may (or may not) be a response to an earlier motion by the prey. This behavioral coupling has the potential to make the behavior of predator or prey appear as a stochastic chain of events. Multivariate statistics are generally insensitive to such dynamics, yet may resolve exceptional

features of successful prey [3] or predators [8]. Such analysis is enhanced by considering behavioral responses to an artificial predator or prey that is experimentally controlled [7,9]. An alternative approach explicitly considers the kinematics of one agent in an attempt to resolve the strategy of the other. For example, bat predators have been shown to track evasive moths by maintaining their heading, rather than attempting to anticipate the prey's direction [10]. This finding was resolved by comparing the measured trajectory of predators to that predicted by a behavioral algorithm, given the measured motion of prey.

The strategic implications of predator and prey behavior have been considered through applications of game theory. This area has capitalized on the development of mathematical modeling in two areas. Biologists concerned with Search games

Such agent-based modeling Predator-prey strategy may alternatively be considered with game theory.

Game theory offers an analytical toolkit for studying the strategic implications of locomotion and sensing . . . cite Weihs' paper, Alberto's paper, Casas... [11,12] AN: Don't know the Casas paper you're talking about Differential game theory, as it has been applied to predator-prey interactions, is purely deterministic and consequently offers the opportunity to resolve optimal strategies by analytical mathematics. . .

The present study addressed the strategic importance of sensing and locomotion using a combination of experiments and mathematical modeling. High-speed kinematics were recorded for the swimming by individual zebrafish larvae as they were pursued by individual adult predators of the same species, as in previous studies [9,12]. Descriptive statistics of these interactions were used to characterize the probability of behavioral actions by both the predator and prey. These findings provided the basis of a game model that was used to simulate the conditions of our experiments. Once verified, an analysis of this model was performed to evaluate the sensitivity of prey survival on the behavioral parameters of the predator and prey.

2. Material and methods

(a) Animal husbandry

All experiments were conducted on zebrafish (*Danio rerio*, Hamilton 1922), where larvae ($5 - 7$ days post fertilization, dpf) were preyed upon by older fish of the same species. To examine how these interactions vary with the size of the predator, we performed one set of experiments using adult (≥ 9 months old, $3.4\,\mathrm{cm} \pm 0.5\,\mathrm{cm}$) predators and another using juveniles ($3 - 4$ months old,

$2.0\,\mathrm{cm} \pm 0.4\,\mathrm{cm}$). Although similar in shape, adults were significantly larger in body length and gape diameter than juveniles (adults: $2.4\,\mathrm{cm} \pm 0.044\,\mathrm{cm}$, juveniles: $2.38\,\mathrm{cm} \pm 0.030\,58\,\mathrm{cm}$, One-way ANOVA, $N = 19$). All fish were bred from wild-type (AB line) colonies housed in a flow-through tank system (Aquatic Habitats, Apopka, FL, USA) that was maintained at $28.5\,^{\circ}\mathrm{C}$ on a 14:10 h light:dark cycle. To produce larvae, the fertilized eggs from randomized mating were cultured according to standard techniques [13]. Predators were motivated to feed by fasting for a period of 7 – 14 days prior to an experiment.

(b) Kinematics

We arranged the lights and cameras for high-speed recordings of both fish with high-contrast images. A hemispherical aquarium ($\oslash = 8.5\,\mathrm{cm}$) was composed of white acrylic, which served as a translucent diffuser of the IR illumination (940 nm) provided by three lamps (CM-IR200-940, CMVision, Houston, TX, USA), positioned below (Fig. 1a). These lamps provided high-intensity illumination that was invisible to the fish [14], while visible illumination at low intensity was provided by overhead fluorescent lights. Each camera (FASTCAM Mini UX50, Precision Photron Inc., San Diego, CA, USA) was fitted with a with a 55mm lens (f/2.8 Micro Nikkor AIS, Nikon Inc., Melville, NY, USA) and positioned at a distance to permit a view of the entire aquarium. The cameras were arranged above the aquarium to allow both fish to be viewed by at least two cameras when the fish were positioned close together. The cameras were synchronized to record at 1,000 fps (at 1024 x 1024 pixels) with a common TTL end-trigger and controlled with the manufacturer's software (PhotronFASTCAM Viewer).

Predation experiments were performed by recording the swimming of one predator and one prey fish in the aquarium (Fig. 1A). This began by placing the fish on opposite sides of a partition. Following a 15 min acclimation period, we lifted the partition and observed the fish until the predator successfully ingested the prey. Using a post-trigger to the high-speed cameras, we saved recordings from $\sim 0.5\,\mathrm{s}$ before the first predatory strike and until $\sim 0.5\,\mathrm{s}$ after the prey was captured.

Our video recordings were used to perform measurements of 3D kinematics. We calibrated the cameras by recording a static body that we constructed with 48 landmarks of known relative position, which was placed in the center of the aquarium. A direct-linear transform (DLT) was calculated using 'Digitizing Tools' software in MATLAB (2015a, MathWorks, Natick, MA, USA) [15] from manually-selected coordinates of these landmarks from the perspective of the three cameras. Using a custom script in MATLAB, we found the body positions of predator and

prey fish by selecting landmarks from two camera views and using the DLT to determine the coordinates in 3D space. We used the position of the predator's two eyes to calculate a mean position that approximated the buccal cavity (Fig. 1a). The rostrum and posterior margin of the swim bladder were found on the prey's body. The posterior of the swim bladder approximates the center of mass [16]. We acquired the landmark positions at five key events in each interaction between predator and prey: (1) when the predator initiated an approach toward the prey, when the predator (2) began and (3) completed suction feeding and (4) at the initiation and (5) completion of the prey's escape response.

(c) Descriptive statistics

Descriptive statistics were used to characterize the probability of actions by the predator and prey during predation experiments. For all interactions recorded among our experiments, we found predator-specific parameters that consisted of the strike distance (s), the distance from the prey at which a strike was initiated, and the strike duration (τ), which is the period between the opening and closing of the mouth during suction feeding. For the prey, we found the reaction distance (l), which is the distance from the predator at which the escape response is initiated. The escape was additionally characterized by the escape angle (θ), the angular change in heading from the resting orientation to the escape path. The escape duration (η) included the period for all stages of the C-start and subsequent undulatory swimming, until the larva ceased motion. The frequency distribution for each parameter was found to be well-approximated by the following log-normal probability density function:

$$f(x) = \frac{1}{x\sigma\sqrt{2\pi}}\exp\left[-\frac{(ln(x)-\mu)^2}{2\sigma^2}\right],$$ (2.1)

where x is a particular behavioral parameter (s, τ, l, θ, or η), μ is the log mean, and σ is the log standard deviation. We determined best-fit values for μ and σ for each behavioral parameter by maximum-likelihood (the 'fitdist' function in MATLAB).

The probability that the strike of a zebrafish predator is successful depends critically on the distance between the mouth and the prey [17]. Strikes were therefore measured as a function of distance. These measurements revealed that the probability of a successful capture (C) was well-characterized by the following sigmoidal function:

$$C(d) = \left[1 + e^{-r(d-d_0)}\right]^{-1},$$ (2.2)

where d is the distance between predator and prey, d_0 is the decay distance, and r is the decay rate. The best-fit values for d_0 and r were determined by least-squares ('sqcurvefit' function in MATLAB).

All parameters for the prey and predators were compared between experiments with adult predators and juvenile predators. These parameters failed to conform to normal distributions, so we performed comparisons with non-parametric statistics. In particular, probability-density functions (Eqn. 2.1) and capture probability (Eqn. 2.2) parameters were compared using a two-sample Kolmogorov-Smirnov test (i.e. KS-test) [18].

(d) Game model

A pursuit-evasion game model was developed to simulate the conditions of our experiments. This model predicted the 2D motion of a predator (i.e. pursuer) and prey (i.e. evader) according to algorithms that were specific to the behavioral state of each of these agents (Fig. 1b). The predator's states were Tracking (T) and Striking (S) and the prey's were Resting (R) and Escaping (E). The duration of states, probability of transitioning between states, and probability of capture were determined by random-number generators with probability distributions and a range of values that matched the results of our kinematic measurements. Therefore, the model treated the predator and prey's actions as probabilistic, but each outcome of an interaction also depended on the determinism of the kinematics of the two agents. Simulations were scripted in MATLAB to calculate the motion of both agents and their behavioral states and consequently determined the number of unsuccessful strikes before prey capture.

Each simulation began with the predator in the Tracking state, where it moved at an approach speed U with a direction that was always headed toward the prey, with perfect information about the prey's position (Fig. 1b). If the prey was motionless, then the solver would advance in time to the strike or escape initiation, whichever was found to occur first. Otherwise, the predator tracked the motion of the prey with a delay, λ, calculated with a fixed time step of $5\,\mathrm{ms}$. The predator's transition into the Striking state occurred when the prey was within a particular distance that was determined by the strike distance (s). This value for was determined *a-priori* by the generation of a random value (using the 'random' function in MATLAB) from the log-normal probability-density function (Eqn. 2.1) for measured values of s. The capture probability for a particular strike depended on the distance between the agents in the middle of a strike, according to our measured parameter values for this relationship (Eqn. 2.2). Our simulations used this relationship to generate a random value for the range within which the prey was determined to be captured.

The simulation was terminated if a strike was successful, otherwise the predator reverted to the Tracking state after completion of the strike duration. Single values for the approach speed and predator delay were used for all simulations (Table 1) and were determined by trial-and-error to best replicate the distribution of the measured number of unsuccessful strikes before prey capture. These values approximated measurements reported in prior studies [17,19].

The game model simultaneously determined the actions of prey (Fig. 1b). Prey behavior was modeled with Resting and Escaping states because larval zebrafish generally remain still between periods of rapid swimming initiated by an escape response [9,17]. The prey began each simulation in the Resting state, where it was motionless at a random distance equal to, or less than, the aquarium diameter ($\oslash = 8.5\,\text{cm}$) and at a random orientation with respect to the predator. The prey transitioned into the Escaping state when the predator moved within the reaction distance (l) after a latency (χ) [20]. During an escape, the prey was assumed to follow a straight path in the direction of the escape angle (θ). Using a frame-by-frame kinematic analysis of escape swimming for 12 larvae, we found that prey varied speed as a saw-toothed function of time that approximately attained its maximum value at 20% of the duration duration. We consequently modeled variation in swimming speed for prey to attain the maximum speed (u) was achieved at 0.2η, where η is the escape duration. The reaction distance, escape angle, and escape duration were determined by random numbers with probability density functions matching experimental measurements. The escape angle was defined with respect to the prey's frame of reference, with $\theta = 0°$ corresponding to forward motion. The escape direction (υ) was defined as the probability that this angle was directed away from the predator, with a value (Table 1) that was previously measured [9].

This model simplified many aspects of the complexity of predator-prey interactions. It assumed that the kinematics of the two fish may be reasonably approximated with two-dimensional motion that is not bounded by an aquarium. Simulations were stopped if prey successfully escaped on 20 occasions, which reflected the observed maximum and guarded against an errant simulation of infinite duration. The model's probabilistic approach considered the effects of biomechanics and neurophysiology without articulating those elements. For example, capture success was treated as a distance-specific probability (Eqn. 2.2) that parsed neither the effects of a predator's suction-feeding hydrodynamics, nor the propulsive forces generated by an escaping prey. The number of successful escapes before capture for all experiments were compared to the same metric for 1,000 simulations. This comparison was

executed by a two-sample Kolmogorov-Smirnov test, chosen over a Kruskal-Wallis test because of its emphasis on the shape of the distribution.

A sensitivity analysis evaluated the characteristics of the predator and prey behavior which had the greatest effect on prey survival. This was achieved by running batches of a 1,000 simulations with parameters varied individually between -90% and 100% of their original mean values at increments of 10%. For parameters described by a probability distribution, the log-mean μ parameter and the range of values were adjusted to create the desired percent-change in the mean of the distribution. The effect of these manipulations were assessed by comparing the measured escape probability against the model's prediction using a Kruskal-Wallis test.

3. Results

(a) Kinematics

The behavior of both predator and prey were similar whether the predators were juvenile or adult zebrafish. Prey responded with similar behavior, having indistinguishable differences in escape angle (KS-test: $P = 0.86$, $N = 164$) and with modest, though significant, differences in reaction distance (KS-test: $P < 0.001$, $N = 164$) and escape duration (KS-test: $P = 0.04$, $N = 153$) (Fig. 2b–c). For example, prey responded at a mean distance to juvenile predators ($\bar{l} = 8.4$ mm, $N = 91$), at about two-thirds the response distance to adults ($\bar{l} = 12.6$ mm, $N = 73$). Escape swimming lasted for about one-third of a second, with the response to juveniles ($\bar{\eta} = 0.35$ s, $N = 91$) being only 50 ms longer than to adults ($\bar{\eta} = 0.30$ s, $N = 62$). Juvenile and adult predators were significantly different in neither their strike distance (KS-test: $P = 0.08$, $\bar{s} = 7.6$ mm, $N = 154$), nor strike duration (KS-test: $P = 0.87$, $\bar{\tau} = 44$ ms, $N = 107$) (Fig. 2d–e). Therefore, much of the behavior of predator and prey were similar, despite the fact that the adults were nearly twice the body length of the juveniles.

The major exception in this comparison was in the effectiveness of strikes by suction feeding. Juveniles did not succeed in capturing prey beyond a distance of 3.2 mm ($N = 91$), whereas adults captured prey at a maximum distance that was 3-times greater (10.4 mm, $N = 77$). In the relationship between capture probability and distance (Eqn. 2.2), the decay distance indicates the spatial range of high capture probability. By this metric, the strike of adult predators also exhibited a range that was slightly greater than 3-times the distance of juveniles (Table 1, Fig. 2f). Therefore, the spatial proximity of suction feeding is the key feature that distinguishes the performance of juvenile and adult predators.

(b) Game model

The trajectories of predator and prey fish followed paths that were qualitatively similar to that predicted by our game model. For most of the duration of our experiments, predators were observed to be swimming toward the prey (Fig. 3a). In contrast, the prey were generally motionless, unless interrupted by undulatory swimming, initiated with a fast-start. The predators and prey followed a more circuitous path toward to prey than the motion prescribed by our model (Fig. 3b). Nevertheless, the temporal sequence of events in the model offered a reasonable approximation of the kinematics of live predator-prey interactions.

The model accurately predicted the broad quantitative patterns of our experimental results. This was assessed by the probability of the prey surviving over a particular number of strikes. In our experiments, prey exhibited the greatest probability of being captured on the first strike with monotonically lesser probabilities over subsequent strikes (Fig. 3c). Adults were more successful on the first, second and third strikes than the juveniles, which consequently exhibited a more even probability distribution. The model was successful in replicating these trends, which were found to be statistically indistinguishable for both adult (KS-test: $P = 0.93$, $N = 73$) and juvenile (KS-test: $P = 0.86$, $N = 91$) predators. Furthermore, all trends from the sensitivity analyses of the game model were similar between the juvenile and adult predators. Therefore, adult game model results are presented in this results section and juvenile predator results from the game model are presented in the supplemental material (Fig. Supp. Mat.).

A sensitivity analysis of prey parameters revealed that escape speed and reaction distance were the only parameters with a substantial effect on prey survival. Changes in escape duration, escape direction, and escape angle led to statistically insignificant or small changes in escape probability (Fig. 4a). In contrast, modulating reaction distance and escape speed changed the escape probability substantially. On average, changes in reaction distance and escape speed created a 23% and 15% greater change in escape probability, respectively, than changes in the other three parameters. By increasing the mean value of the reaction distance, escape probability increased significantly by upwards of 16%. However, decreasing the mean value of the reaction distance created greater, significant decreases to the escape probability, as great as 70% with a 90% decrease in the reaction distance. Increasing escape speed did not lead to a significant increase in escape probability and significant decreases to escape probability only occurred when escape speed was reduced by 50% or more of its original value.

We examined whether escape speed and reaction distance interactively affect escape probability by conducting a two-dimensional sensitivity analysis (Fig. 4b). This yielded results

which were consistent with our initial analysis (Fig. 4*a*). For a particular escape speed, increasing reaction distance above the measured value slightly, though significantly, increased the overall escape probability. However, a decrease in reaction distance generated large decreases in escape probability (Fig. 4*c*). For example, at the measured escape speed value, increasing the reaction distance by 30% of its mean value increased the escape probability by 6.6%. Conversely, decreasing the reaction distance by 30% at the same escape speed generated a 18.7% decrease in escape probability. Increasing escape speed while the reaction distance was held constant did not substantially increase escape probability (< 2% increases in escape probability, on average). However, decreasing the escape speed by 70% led to a 43% change, on average, throughout all tested values of reaction distance.

4. Discussion

The present study succeeded in developing a game model for the spatial interactions between predator and prey fish. This model replicated the broad patterns in the survival of prey (Fig. 3*c*) by incorporating measured probabilities of behavioral events (Fig. 2) in formulating predicted kinematics (Fig. 3*b*). A sensitivity analysis of this model revealed that prey survival varies acutely with reaction distance and, to a lesser degree, escape speed.

Increasing reaction distance and escape speed have diminishing returns to escape probability. As shown in the one-dimensional analysis (Fig. 4a), increasing reaction distance and escape speed had a marginal effect on escape probability. Yet, decreasing either parameter greatly lessened the chance for a prey to escape a strike. These trends still persist when the data is expressed as the number of predator strikes before capture (Fig. Supp. Mat.), rather than a percentage.

Escape speed has a "threshold" motif, where increasing escape speed beyond a certain value yields no extra payoff. In fact, the performance threshold value, based off the one-dimensional sensitivity analysis, would be around 50% of the measured value. This suggests larval zebrafish are performing well beyond this performance threshold. The innate escape speed in larval zebrafish could act as a performance buffer. Escape speed can be quite variable and having a performance buffer can offset the the detrimental effects of escape speed variability.

Reaction distance follows a similar trend as escape speed; though increasing reaction distance can confer some benefit. Like escape speed, decreasing reaction distance can greatly decrease the chance of a prey escaping. However, unlike escape speed, increasing the mean reaction distance confer marginal, but significant, increases to escape probability. Therefore, there is a beneficial effect in increasing the range of the receptive field of the prey. One explanation why the benefit

is so marginal is that the game model start the prey within a finite distance from the predator. Increasing the reaction distance much further than this set distance (8.5 cm) would not confer much benefit. Moreover, reacting too far away can also be detrimental [17]. Often when prey initiate an escape farther away from the predator, the predator can readjust its approach to compensate for the early initiation of the escape.

From the results of this study, sensing the predator is the most impactful parameter. Our sensitivty analyses examined five different parameters involved in sensation and locomotion of the prey. Amongst all of them, reaction distance had the largest impact on escape probability. Escape angle, direction, duration, and speed are parameters involved in how the prey locomote away from the predator. Of those four parameters, only escape speed had a major impact on how successful a prey was in escape predator strikes. As described earlier, the effects of escape speed on escape probability are somewhat limited as increasing it confers no benefit. Reaction distance describes the summative abilities of all the prey' senses to detect a threat from a certain distance away from the predator. Modulation of the reaction distance was able to create significant increases and decreases in escape probability, unlike escape speed. This suggests that affecting this parameter can create the widest array of changes to the outcome of a predator-prey interaction. Realistically, reaction distance can be altered in a number of ways. Physiological evolution can occur over many generations to increase reaction distance. Conversely, Turbid or dark environments can also limit the reaction distance if the prey heavily relies on vision.

The findings of the present study are not anticipated to be generally predictive for all predator-prey interactions. Differential game theory illustrates that prey strategy fundamentally depends on the relative magnitude of escape speed relative to the predator [11]. Like many suction-feeding predators [21,22], larger zebrafish approach prey at a relatively slow speed, perhaps in an attempt to control the short-lived and spatially-restricted suction-feeding strike. As a consequence, the escape response of larval zebrafish exceeds the speed of the larger predator. This permits the prey to escape over a range of directions that are equally successful at maximizing the distance from a predator [12]. In this context, it is unsurprising that escape direction has an insignificant effect on prey survival (Fig. 4a). However, the same is unlikely to hold true for faster predators. Although escape angle matters little in instances when the predators is more than an order-of-magnitude faster than the prey, escape direction conforms to an optimal value in instances with the predator is only slightly faster than the prey [11]. We therefore would anticipate different results for faster predators than the adult zebrafish that we studied.

Our model has the potential to provide broad implications for the biology of fishes and for predator-prey interactions in general. Our game model can abstractly model many different predator-prey interactions amongst fish and other animals. For many interactions between a predator and "burst movement" prey, such as larval zebrafish, our model can describe a first order approximation the interaction with a simple change in parameter values. For other predator-prey interactions, our model can be easily expanded and/or modified to include extra behavior for the predator and prey. For instance, the virtual prey can have a Roaming state instead of a Waiting state. In the Roaming state, the prey can randomly move as it meanders through space. Two probability distributions can be related to the Roaming state, a roam angle and duration, which dictate how the prey moves through space and with what intervals. These probability distributions, like the ones in the current model, can be constructed through observations of idle prey.

Outtakes

Differences between successful escapes and failed escapes in each prey or predator parameter were insignificant (Mann-Whitney U test: P > 0.05, N = see Table 1). This suggested that neither locomotion or sensing had an significant impact on whether a prey escape attempt was successful or not.

This seemed unreasonable since it well known both sensory and motor systems are important for prey survival (CITE). We suspect this discrepancy emerged from the fact that the behavior of predator zebrafish and larval zebrafish were dependent on each other. This led to a coupled system of behavior where there were not strict measurable controls. Therefore, we decided to computationally model the observed predator-prey interactions, allowing the ability to control for various aspects of the predatory encounter. MAKE THIS OF A MORE THEORETICAL STANCE.

Data accessibility

Authors' contributions

The study was designed in collaboration between AN and MJM. AN and CN performed all experiments and kinematic analysis. The game model was created by AN, with guidance from MJM. The manuscript was written collaboratively by AN and MJM.

MJM:I'm not clear on what data to which the following is referring. Can we dispense with this? I don't think we need to include mention of the failure of conventional stats.

AN:This is comparing just the experimental data between successful and failed strikes. This shows that with just experiments, we cannot see what parameters are important to prey survival.

This reads to me like Methods, or maybe Discussion text. Ditch?

AN: Yes, it does seem like its an odd place

Competing interests

We declare we have no competing interests.

Funding

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Acknowledgments

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Table 1. Behavioral parameters and probability distributions

Variable	State	Adult predator	Juvenile predator
Predator			
Approach speed, U (m s^{-1})	T	$U = 0.13$	$U = 0.05$
Predator delay, λ (ms)	T	$\lambda = 10$	$\lambda = 10$
Strike distance, s (m)	T → S	$\mu_d = -4.980$, $\sigma_d = 0.448$ ($N = 51$)	$\mu_d = -5.100$, $\sigma_d = 0.648$ ($N = 103$)
Strike duration, τ (s)	S	$\mu_\tau = -3.166$, $\sigma_\tau = 0.331$ ($N = 53$)	$\mu_\tau = -3.208$, $\sigma_\tau = 0.399$ ($N = 54$)
Capture probability, C	S	$r = 0.573$, $d_0 = 5.20$ ($N = 77$)	$r = 1.99$, $d_0 = 1.60$ ($N = 91$)
Prey			
Reaction distance, l (m)	R → E	$\mu_l = -4.546$, $\sigma_l = 0.587$ ($N = 73$)	$\mu_l = -4.941$, $\sigma_l = 0.582$ ($N = 91$)
Escape angle, θ (rad)	E	$\mu_\theta = 0.144$, $\sigma_\theta = 0.449$ ($N = 206$)	$\mu_\theta = 0.144$, $\sigma_\theta = 0.449$ ($N = 206$)
Escape duration, η (s)	E	$\mu_\eta = -1.369$, $\sigma_\eta = 0.552$ ($N = 62$)	$\mu_\eta = -1.167$, $\sigma_\eta = 0.5234$ ($N = 91$)
Escape direction, υ	E	$\upsilon = 0.696$ ($N = 206$)	$\upsilon = 0.696$ ($N = 206$)
Escape latency, χ (ms)	E	$\chi = 8$ ($N = 15$)	$\chi = 8$ ($N = 15$)
Escape speed, u (m s^{-1})	E	$u = 0.4$ ($N = 12$)	$u = 0.4$ ($N = 12$)

T, Tracking; S, Striking; R, Resting; E, Escaping; μ, log mean; σ, log standard deviation; r, decay rate (mm^{-1}); d_0, decay distance (mm).
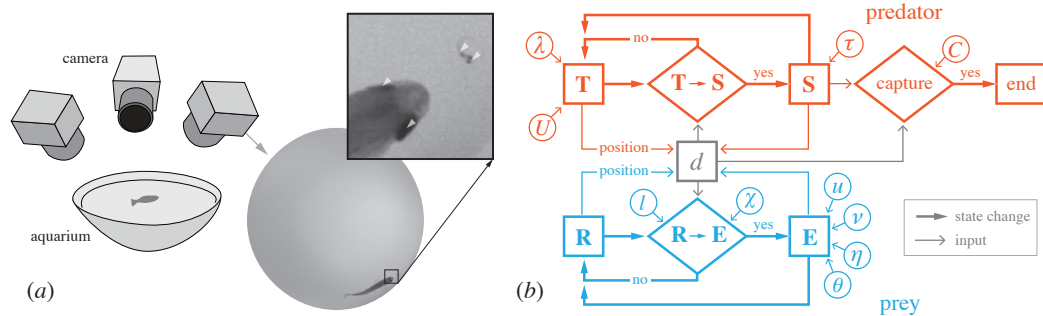
Figure 1. Experimental and mathematical techniques for studying predator-prey interactions. (*a*) Three high-speed video cameras recorded video of one larval prey and one adult predator fish that were placed in a hemispherical aquarium. A representative video frame (cropped to the margin of the aquarium) shows an adult in close proximity to the prey. In the inset, white triangles denote the locations of morphological landmarks used to describe the position of the two fish. (*b*) A flow chart illustrates the major components of the game model used to simulate the interactions between predators and prey (see Table 1 for symbol definitions and parameter values).
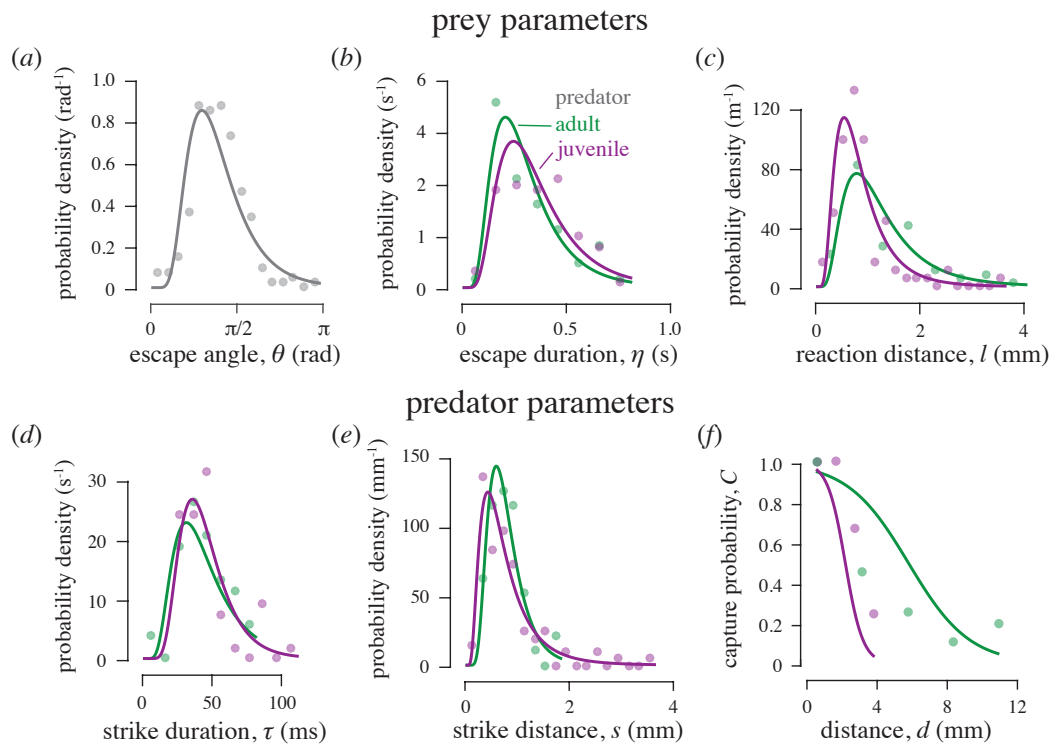
Figure 2. Descriptive statistics of swimming kinematics. (*a-e*) The probability density measurements (circles) and function (Eqn. 2.1) fit for experiments where the predator was a juvenile (purple) or adult (green) predator, which were significantly different, except for escape angle (*a*), shown in gray. Parameters were measured from the kinematics of prey (*a-c*) and predators (*d-e*). (*f*) The capture probability was examined as it varies with distance between the predator and prey (Eqn. 2.2).
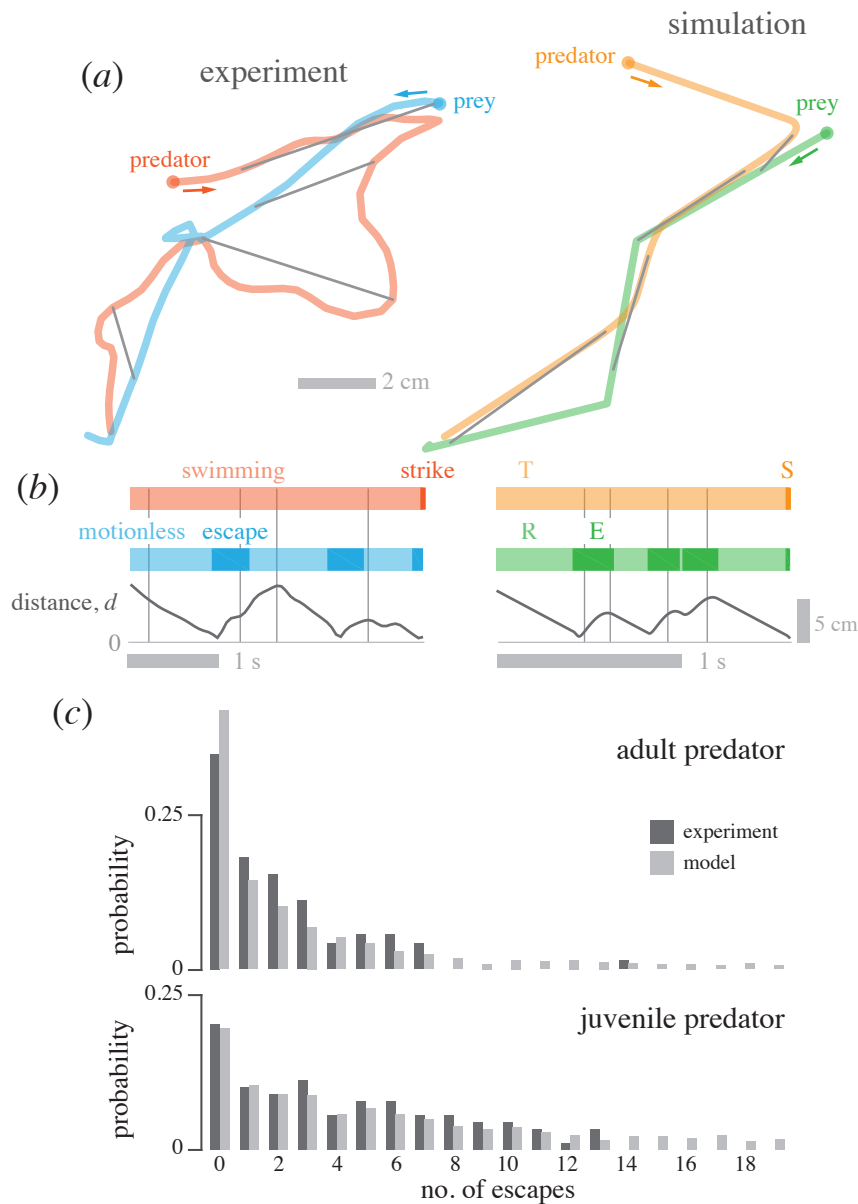
Figure 3. Comparison between experimental measurements and mathematical modeling. (*a*) Trajectories of predator and prey from a representative experiment (left) and simulation (right). (*b*) Ethograms for these trajectories illustrate the temporal changes in the predator's swimming and strike (left), which are respectively modeled by the T and S (Fig. 1*b*) modes (right). The prey's behavior while motionless and during escape (left), where modeled with the R and E modes of the model (right). For both ethograms, the distance between predator and prey are shown and particular moments in the trajectories are highlighted with vertical gray lines. (*c*) The probability that a prey survives over a particular number of strikes is shown for when the predator was and adult (above) and juvenile (below) for experiments and model simulations.
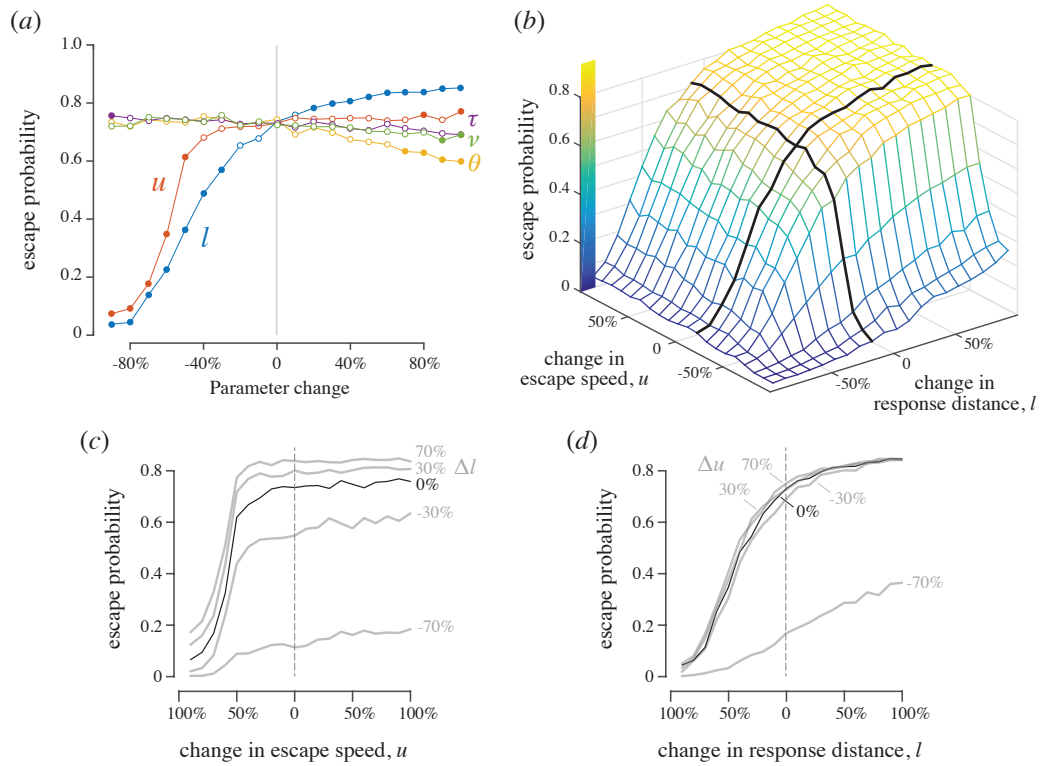
Figure 4. Sensitivity analysis of game model to examine the effects of parameter variation on escape probability. (*a*) Varying the the mean of the distribution by manipulating the log-mean value (see Table 1 for parameter definitions and values), with each point representing the result of 1000 simulations. (*b*) Variation in escape probability was examined with respect to both escape speed and response distance the same simulation results are shown with respect to changes in escape speed (*c*) and response distance (*d*).