

¹ Escape direction does not matter for some fish prey

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4

Abstract

5 Predator-prey interactions are commonly studied with an interest in determining
6 whether animals behave with optimal strategy. However, the consequences of optimal
7 strategy are largely unclear. Here we examine the strategic effects of deviating from
8 optimal strategy in fish that are preyed upon by fish predators. We simulated these
9 interactions with numerical and analytical mathematics and compared our predictions
10 with measurements in zebrafish (*Danio rerio*). As in previous models, we focused on
11 the effect of the escape direction on the minimum distance between predator and prey.
12 We found that differences in escape direction had only a small effect on the minimum
13 distance when predators were more than an order of magnitude faster than the prey.
14 Furthermore, differences in direction had no effect on performance for a broad range
15 of escape angles when the prey were faster than the predator. Therefore, an optimal
16 strategy may not exist or offer little benefit when the predator is either slower or much
17 faster than the prey. The optimal prey strategy is consequently most meaningful when
18 approached by a predator of intermediate speed. This demonstrates that the speed
19 of a predator relative to the prey provides a key index of predator-prey strategy that
20 indicates when optimal solutions are effective.

21 1 Introduction

22 Biologists have long—appreciated the importance of predation in the ecology and evolution
23 of prey species. This subject is extensive enough to fill the pages of books on the fasci-
24 nating diversity of strategies that prey use to avoid encounters with predators (e.g. Ruxton
25 et al., 2004) or to defend themselves when discovered (e.g. Emlen, 2014; Evans and Schmidt,
26 1990). In contrast, our understanding for how prey evade capture by locomotion is relatively
27 rudimentary. Although biomechanical studies commonly speculate on the importance of lo-
28 comotor performance to survival, relatively few have tested what aspects of locomotion are
29 most meaningful in these interactions. Studies that have explored this subject (reviewed by
30 Domenici and Blagburn, 2011) underscore the common-sense notion that the direction of an
31 escape matters to a prey’s survival. This idea is formalized by pursuit-evasion models that
32 aim to determine the optimal direction of an escape response. The present study examined
33 such a model, based on Weihs and Webb (1984a), to consider the strategic consequences of
34 deviating from optimal strategy in piscivorous interactions. We compared the model’s pre-
35 dictions to experimental results in zebrafish (*Danio rerio*) (Stewart et al., 2014) and arrived
36 at new interpretations of theory on prey strategy.

37 Pursuit—evasion models are an area of differential game theory that offers a basis for
38 examining locomotor behavior in strategic terms. There is recent interest in revisiting these
39 models (e.g. Howland, 1974; Weihs and Webb, 1984a) with experimental studies that consider
40 the behavior of both predators and prey. This includes work on running vertebrates (e.g.
41 Wilson et al., 2013), birds (e.g. Kullberg et al., 1998) and bats (e.g. Ghose et al., 2006) in
42 flight, running insects (Domenici et al., 2008), flying insects (e.g. Combes et al., 2012), and

43 swimming zooplankton (e.g. Arnott et al., 1999; Heuch et al., 2007) and fishes (e.g. Domenici
44 et al., 2000; Holzman et al., 2011). Other applications of game theory have also recently
45 been applied to search strategy in parasitoid wasps (Gal and Casas, 2014; Djemai et al.,
46 2010). These efforts offer the potential to reveal how sensory and motor systems govern the
47 outcome of predator-prey interactions.

48 A piscivorous interaction offers some advantages as a model for predator-prey interac-
49 tions. In many cases, this behavior can be easily studied in a laboratory, where predatory
50 fishes attempt to feed on prey and prey initiate a ‘fast-start’ escape response (Fig. 1). Both
51 players operate with motion that is largely two-dimensional and therefore relatively simple
52 to measure and describe. Zebrafish adults prey on larvae of the same species with suction
53 feeding in the lab (Stewart et al., 2013) and this species offers a growing wealth of under-
54 standing in physiology and neuroscience (e.g. McLean and Fethcho, 2011; Briggs, 2002) that
55 may be leveraged for mechanistic insight. In addition, fish offer one of the few biological
56 pursuit systems that has been mathematically modeled (Weihs and Webb, 1984a). This
57 model offers specific predictions of swimming trajectories that may be tested with kinematic
58 measurements.

59 Deviation from optimal strategy has been interpreted as a strategic adaptation. The
60 protean hypothesis suggests that prey that are unpredictable have an advantage in predator
61 evasion over unsurprising prey (Humphries and Driver, 1970). This idea may apply to
62 the erratic motion of an individual or a population of prey that collectively exhibit variable
63 motion that challenges a predator’s ability to learn or adapt. The fast start of a fish generates
64 a turn and acceleration of the body in a particular direction and therefore would appear to
65 correspond to the latter category (Weihs, 1973). Regardless, a potential trade-off exists

66 between behaviors that are optimal or unpredictable.

67 Interpretations of prey motion have generally not considered the implications of deviating
68 from optimal strategy. For example, it is not clear whether an escape that is 5° or 50° from
69 the optimum predicted by Weihs and Webb (1984a) has a major or negligible effect on
70 evasion success. If evasive performance is insensitive to differences in escape direction, then
71 no trade-off will exist between evasiveness and predictability. It is unclear if such conditions
72 exist and consequently when optimal strategy matters. The present study therefore revisited
73 the mathematics of the Weihs and Webb (1984a) model to examine how deviation from
74 optimal strategy affects prey evasion. We expanded this model and performed numerical
75 simulations for comparison with experimental results. In this effort, we identified conditions
76 where the escape direction is predicted to have little or no effect on the evasiveness of prey.

77 2 Optimal prey strategy

78 The Homicidal Chauffeur is the colorful title for a pursuit–evasion game that has been applied
79 to a variety of systems, including predator–prey interactions (Isaacs, 1965). Pursuit–evasion
80 games consider the trajectories of its players and thereby address the effects of directional
81 decision–making to the outcome of an interaction. Weihs and Webb (1984) adopted the
82 Homicidal Chauffeur to model the responses of a prey fish that encounters a predator fish.
83 Here we offer a brief review of this model as a means to explain the basis for our expansion
84 of the theory and our interpretations of prey strategy, though a more complete derivation is
85 presented in the original study (Weihs and Webb, 1984a).

86 The payoff is a quantity used in game models to define the beneficial or detrimental

consequences of playing with a particular strategy (Webb, 2007). For the Homicidal Chauffeur, the payoff is often defined as the minimum distance between predator and prey. This quantity reflects the condition where the predator has the best opportunity to capture the prey. The optimal strategy for an evasive prey is therefore defined as the escape angle that yields the greatest minimum distance (Weihs and Webb, 1984).

Predicting the distance between predator and prey requires relatively few parameters under some simplifying assumptions. In the rapid events of a predatory strike, it is reasonable to approximate the predator's motion as a constant speed, U . If one neglects the brief acceleration period (20 ms) of the fast start , then the prey's motion may also be approximated with a constant speed, V , at an escape angle α , defined with respect to the heading of the predator (Fig. 2A). Under these conditions, the distance between predator and prey, D , may be calculated over time:

$$D^2 = ((X_0 - Ut) + Vt \cos \alpha)^2 + (Vt \sin \alpha)^2, \quad (1)$$

where X_0 is the starting position of the prey.

The minimum distance, the payoff in this game, may be calculated from the distance equation. The first step is to calculate the time, t_{\min} , at which the minimum distance occurs. This may be found from the root of the derivative of Eqn. 1 with respect to time, which yields the following equation:

$$t_{\min} = \frac{X_0}{V} \frac{K - \cos \alpha}{1 - 2K \cos \alpha + K^2}, \quad (2)$$

where K indicates the speed of the predator relative to the prey ($K = U/V$).This equation yields negative values of time where $K < 1$ and therefore only applies where $K > 1$. The

¹⁰⁶ minimum distance was consequently determined for $K > 1$ by solving for distance (Eqn. 1)

¹⁰⁷ at t_{\min} :

$$\overline{D}_{\min}^2 = \frac{D_{\min}^2}{X_0^2} = \frac{\sin^2 \alpha}{K^2 - 2K \cos \alpha + 1}, \quad (3)$$

¹⁰⁸ where \overline{D}_{\min} is the minimum distance normalized by the starting position of the prey.

¹⁰⁹ Finally, the optimal strategy for the prey may be determined by finding the escape angle

¹¹⁰ that yields the greatest minimum distance. This occurs where the derivative of Eqn. 3 with

¹¹¹ respect to α is equal to zero, which is explicitly described by the following equation:

$$0 = \frac{\partial \overline{D}_{\min}^2}{\partial \alpha} = \frac{2 \sin \alpha \cos \alpha (K^2 - 2K \cos \alpha + 1) - 2K \sin^3 \alpha}{(K^2 - 2K \cos \alpha + 1)^2}. \quad (4)$$

¹¹² Among the solutions that satisfy this equation, Weihs and Webb proposed that the following

¹¹³ indicates the optimal strategy when the predator is faster than the prey ($K > 1$):

$$\alpha_{\text{opt}} = \pm \arccos K^{-1}. \quad (5)$$

¹¹⁴ We added the \pm symbol to this expression to indicate that prey are equally effective if

¹¹⁵ escaping at an optimal angle toward the left ($\alpha > 0$), or right ($\alpha < 0$) of the predator's

¹¹⁶ heading. For relatively fast prey ($K < 1$), Weihs and Webb suggested that the optimal

¹¹⁷ solution consists of swimming directly away from the predator ($\alpha = 0$) (Weihs and Webb,

¹¹⁸ 1984). Therefore, for any predator speed, this model offers predictions for how a prey can

¹¹⁹ direct its escape to maximize its chances for survival by creating the greatest distance from

¹²⁰ a predator.

₁₂₁ **3 When optimal strategy matters**

₁₂₂ An optimum adopts a different meaning if it corresponds to a sharp global maximum, a
₁₂₃ local peak much smaller than the global maximum, or a shallow peak in performance. We
₁₂₄ considered the conditions exist that surround optimal strategy by calculating how the payoff
₁₂₅ in this pursuit model, the minimum distance (Weihs and Webb, 1984a), varies with escape
₁₂₆ angle and the relative speed of the predator. As an alternative to analytical mathematics, we
₁₂₇ first formulated this performance landscape with a numerical approach that is simple enough
₁₂₈ to execute in a spreadsheet, but which we implemented in Matlab (v2014b, MathWorks,
₁₂₉ Natick, MA, USA). This was done by defining a series of time values at a regular interval,
₁₃₀ which was used to calculate the positions of the predator ($X_{\text{pred}} = Ut$, $Y_{\text{pred}} = 0$) and prey
₁₃₁ ($X_{\text{prey}} = Vt \cos \alpha$, $Y_{\text{prey}} = Vt \sin \alpha$). The minimum value of the distance between them was
₁₃₂ determined in this way for variable escape angle and predator speed, over a range of K and
₁₃₃ α values (Fig. 2B). This yielded results that were coincident with the analytical equation
₁₃₄ for \bar{D}_{\min} formulated by Weihs and Webb (1984) for relatively fast predators ($K > 1$, Eqn.
₁₃₅ 3). However, the advantage of this numerical calculation was that it allowed us to examine
₁₃₆ variation in the minimum distance for slower predators (i.e. $K < 1$) as well. The resulting
₁₃₇ performance landscape (Fig. 2B) illustrates how the minimum distance varies over a broad
₁₃₈ range of values in the relative speed of the predator.

₁₃₉ Our results suggest that the fast start is unlikely to be effective at any escape angle when
₁₄₀ a prey is approached by a very fast predator. For example, if a predator is an order of
₁₄₁ magnitude faster than its prey (i.e. $K = 10$), then the prey can do no better than displace
₁₄₂ its body by 10% of its initial distance (Fig. 2B). In addition, differences in escape angle have

143 little effect on the minimum distance. Specifically, an escape that is 24.5° larger or smaller
 144 than the optimum yields a minimum distance that is less than the value at the optimum
 145 by 0.1 (i.e. 1% of the starting position of the prey). These metrics become increasingly
 146 unfavorable for the prey when approached by an even faster predator (Fig. 2B). At these
 147 speeds, inaccuracy in the feeding strike is likely a more decisive factor to prey survival than
 148 anything the prey may do in response.

149 A different picture emerges when one considers prey that move more quickly than their
 150 predators (i.e. $K < 1$). This condition occurs when predators brake or glide slowly on their
 151 approach toward a prey (Higham, 2007; Higham et al., 2005) while the prey initiates a rapid
 152 escape. For a variety of escape angles, the fast start of these prey cause the predator to
 153 reach no closer than the starting distance (i.e. $\bar{D}_{\min} = 1$, Fig. 2B). In order to define the
 154 bounds of this domain, it is useful to consider the first derivative of the distance function
 155 with respect to time (see Supplemental Materials for details):

$$\frac{\partial D^2}{\partial t} = 2(t(U^2 + V^2) - UX_0 + V(X_0 - 2tU)\cos\alpha). \quad (6)$$

156 An optimal escape ($\bar{D}_{\min} = 1$) can be achieved if the distance function increases for all time
 157 (i.e. $\frac{\partial D^2}{\partial t} \geq 0$). This holds true for $\alpha = 0$, which Weihs and Webb proposed as the optimal
 158 direction (Weihs and Webb, 1984). However, it also holds true that distance increases for
 159 another solution to Eqn. 4 ($\alpha = \pm \arccos K$) and all values in between (see Supplemental
 160 Materials for details). Therefore, the following defines the domain of optimal directions when
 161 the prey is faster than the predator ($K < 1$):

$$\bar{D}_{\min} = 1 \quad \text{if} \quad |\alpha| \leq \arccos(K). \quad (7)$$

162 This analysis suggests that if the escape response of a prey is capable of exceeding the

₁₆₃ approach speed of the predator, then a wide range of angles yield equally successful escapes
₁₆₄ for the prey and thereby define a performance plateau.

₁₆₅ The domain where the optimal strategy matters the most resides between where the prey
₁₆₆ and predator are equivalent in speed and where the predator is an order of magnitude faster
₁₆₇ ($1 < K < 10$). In this domain, prey are capable of attaining appreciable minimum distance
₁₆₈ values and there is a penalty in minimum distance for deviating from the optimal angle (Fig.
₁₆₉ 2B). Therefore, a prey fish has a strong incentive to conform to the optimal prediction when
₁₇₀ encountering a predator that can move slightly faster than itself.

₁₇₁ 4 Comparing models with measurements

₁₇₂ We were interested in examining whether optimal strategy matters under experimental con-
₁₇₃ ditions. This was addressed with recent measurements on larval zebrafish, which were preyed
₁₇₄ upon by adults of the same species (Stewart et al., 2013). This work included experiments
₁₇₅ that used a robot to simulate the approach of a predator toward prey in the dark, with
₁₇₆ recordings of the position at which the prey responded with a fast start and the direction of
₁₇₇ that response (Stewart et al., 2014). This evasive action was stimulated by the lateral line
₁₇₈ system of the prey, which detected the water flow generated by the approaching predator.

₁₇₉ As detailed above, the predictions of the model depend on the speed of the predator
₁₈₀ relative to the prey. The approach speed of the robot, and consequently K , was varied to
₁₈₁ span the range of values observed for a live predator (Stewart et al., 2013). Our calculations
₁₈₂ of K used a prey speed ($U = 22 \text{ cm s}^{-1}$) from the literature that approximates the maximum
₁₈₃ value attained during a fast start for larvae of this species (Budick and O’Malley, 2000; Müller

¹⁸⁴ and van Leeuwen, 2004). As a consequence of the relatively slow approach made by these
¹⁸⁵ suction-feeding predators, the prey had the potential to move faster at all approach speeds,
¹⁸⁶ which yielded K -values that were uniformly less than unity (Fig. 3A).

¹⁸⁷ One discrepancy between the model and our experiments was that the majority of prey
¹⁸⁸ fish did not exhibit an initial position that was aligned with the heading of the predator
¹⁸⁹ robot. This condition has biological relevance because it corresponds to a situation where
¹⁹⁰ a predator fails to approach a prey with perfect accuracy. We therefore modified the Weihs
¹⁹¹ and Webb model by adding a lateral component to the initial position of the prey in our
¹⁹² distance function. Following the same procedure (Eqns. 2–3), we arrived at a minimum
¹⁹³ distance function (see Supplemental Materials for details). This function was simplified by
¹⁹⁴ the use of polar coordinates, as in the following equation:

$$\overline{D}_{\min}^2 = \frac{D_{\min}^2}{R_0^2} = \frac{(\sin(\alpha - \theta_0) + K \sin \theta_0)^2}{K^2 - 2K \cos \alpha + 1} \quad (8)$$

¹⁹⁵ where R_0 and θ_0 are the initial radial and angular positions of the prey relative to the mouth
¹⁹⁶ of the predator (Fig. 2A). Numerical solutions to this equation showed a broad range of
¹⁹⁷ angular positions and escape angles that defined a performance plateau where $D_{\min} = 1$
¹⁹⁸ (Fig. 3B). We found the margins of this plateau using a similar procedure as outlined above
¹⁹⁹ (Eqn. 4). Specifically, we solved for the conditions where the derivative of the minimum
²⁰⁰ distance with respect to α was equal to zero:

$$0 = \frac{\partial \overline{D}_{\min}^2}{\partial \alpha} = \frac{2(K \cos \alpha - 1)(K \cos \theta_0 - \cos(\alpha - \theta_0))(K \sin \theta_0 + \sin(\alpha - \theta_0))}{(K^2 - 2K \cos \alpha + 1)^2}, \quad (9)$$

²⁰¹ We found the solutions that satisfy this equation by setting the terms in the numerator equal
²⁰² to zero. The solution for $K > 1$ and $\theta_0 < \arccos(K^{-1})$ was similar to Eqn. 5, though the

203 initial angular position determines the sign of the optimal angle:

$$\alpha_{\text{opt}} = \frac{\theta_0}{|\theta_0|} \arccos(K^{-1}). \quad (10)$$

204 This solution indicates that the same optimal direction exists when the predator is faster
205 than the prey, irrespective of the prey's initial position up to an initial angular position of
206 90° . As detailed above, we found that the escape angle is equally effective (i.e. $\bar{D}_{\min} = 1$)
207 when the prey is aligned with the predator for a broad range of values (Eqn. 7). This result
208 holds true when prey are positioned lateral to the predator, but this performance plateau
209 depends on the initial angular position of the prey. We found that the following equation
210 defines the bounds of this plateau among the solutions that satisfy Eqn. 8 for $K < 1$:

$$\bar{D}_{\min} = 1 \quad \text{if} \quad |\alpha - \theta_0| \leq \arccos(K \cos \theta_0), \quad (11)$$

211 This demonstrates that the performance plateau reduces in area with increasing predator
212 speed (Fig. 3B). Therefore, fewer combinations of starting positions and escape angles yield
213 equivalent escape performance for faster predators.

214 Using this formulation of the pursuit–evasion model, we evaluated how the measured
215 responses of prey compared to the model predictions (Fig. 3C). This revealed that the vast
216 majority of larvae operated within the performance plateau and therefore were predicted
217 to yield maximal performance ($\bar{D}_{\min} = 1$). This was true even at the fastest predator
218 approach speed ($K = 0.90$), where the performance plateau encompasses a smaller area of
219 the performance landscape. Therefore, the large variation in observed escape direction incurs
220 no penalty in the evasive performance of most larvae.

221 **5 Predator strategy**

222 Although the present pursuit–evasion models were formulated with a focus on prey fish, they
223 provide the opportunity to consider the strategy of fish predators. The payoff considered by
224 these models is normalized by the initial response distance of the prey (Figs. 2–3). Because
225 the absolute distance traversed is therefore predicted to be proportional to the initial response
226 distance, the predator may first do well to minimize this distance. This may be achieved by
227 moving with a slower approach to reduce the stimulus intensity for the visual (Dill, 1974) and
228 lateral line (Stewart et al., 2014) systems that could startle the prey. This is one benefit to
229 the braking behavior that suction–feeding predators exhibit before a strike (Higham, 2007;
230 Higham et al., 2005). Another advantage to a slow approach is the potential for greater
231 accuracy in the timing and direction of a suction–feeding strike, which is restricted to a brief
232 duration over a relatively small region around a predator’s mouth (Wainwright et al., 2001).

233 Our results also indicate some of the strategic advantages for fast predators. Moving
234 faster than the escaping prey greatly diminishes the escape angles that are beneficial for
235 evasion (Fig. 2B). As we discussed above (in “Optimal prey strategy”), the fast start can
236 become ineffective at offering any benefit to predator evasion when the predator is substan-
237 tially faster and headed directly at the prey. However, such a high–speed approach may
238 present a challenge for a predator to coordinate the timing of the strike (Higham, 2007;
239 Higham et al., 2005).

240 We conducted a series of simulations that examine the effect of an inaccurate strike by
241 a fast predator. As in our comparison with experimental results (Fig. 3), we calculated
242 the minimum distance for a range of values in escape angle and initial position, but this

time considered predators that were faster than prey ($K > 1$). We interpreted deviation from a zero angular position as a measure of inaccuracy in the strike of the predator with the assumption that fish lack the interception targeting used by bats (Ghose et al., 2006) and birds (Kane and Zamani, 2014). This measure of inaccuracy neglects the increasing challenge of correct timing in the opening of the jaws at increasing approach speeds (Kane and Higham, 2014, 2011), but does address errors in the direction of the approach.

The results of these simulations illustrate the relative contribution of escape angle and strike accuracy on evasion for different approach speeds. For a predator that is twice as fast as the prey ($K = 2$), the minimum distance varied substantially with both escape direction and strike accuracy (Fig. 4A). For example, the optimal escape angle ($\alpha_{\text{opt}} = 60.0^\circ$) generated a minimum distance ($\bar{D}_{\text{min}} = 0.71$) that was more than two-orders of magnitude better than what was achieved with the least effective escape direction ($\bar{D}_{\text{min}} = 0.002$) when the prey is positioned 15° from the predator's heading. This advantage in minimum distance was not greatly reduced ($\bar{D}_{\text{min}} = 0.50$ at $\alpha_{\text{opt}} = 60^\circ$) if the predator successfully aligned its strike ($\theta_0 = 0^\circ$). However, the escape angle played a reduced role in aiding predator evasion at faster approach speeds. For example, when the predator was 10-times faster (Fig. 4C) and inaccurate ($\theta_0 = 15^\circ$), then the optimal escape angle ($\alpha_{\text{opt}} = 84.3^\circ$) was only slightly more than twice the value ($\bar{D}_{\text{min}} = 0.35$) for the least effective angle ($\bar{D}_{\text{min}} = 0.16$). Furthermore, the optimal minimum distance ($\bar{D}_{\text{min}} = 0.10$) was relatively ineffective for an accurate strike ($\theta_0 = 0^\circ$). Therefore, the accuracy of a predators' strike becomes an increasingly dominant factor in determining prey survival with predators that are many times faster than the prey.

₂₆₄ **6 Conclusions**

₂₆₅ We have identified situations where optimal strategy matters little to the outcome of a
₂₆₆ predatory strike. These situations depend on the relative speed of the predator and prey,
₂₆₇ which underscores the coupled nature of pursuit strategy. When a predator approaches
₂₆₈ relatively slowly, prey have the opportunity to escape in a variety of directions (Figs. 2B,
₂₆₉ 3B–C). When they strike quickly, the accuracy of the predator’s heading becomes a major
₂₇₀ determinant in the outcome (Fig. 4).

₂₇₁ It may appear counter-intuitive that any predator would move more slowly than its
₂₇₂ prey. Predatory fishes are commonly between 2- and 20-fold greater in length than prey fish
₂₇₃ (Fuiman, 1994) and are generally capable of swimming many times their body length per
₂₇₄ second by rapid undulation (Bainbridge, 1958). However, fishes also exhibit a large scope of
₂₇₅ swimming speeds and may move slowly by the coordinated braking action of their many fins
₂₇₆ (Videler, 1981; McHenry and Lauder, 2005). Many suction-feeding predators take advantage
₂₇₇ of this hydrodynamic plasticity to slow swimming on the approach of a feeding strike. This
₂₇₈ braking results in swimming that is in the lower range of potential speeds, at rates below a
₂₇₉ single body length per second (Higham et al., 2005; Higham, 2007). In contrast, a startled
₂₈₀ prey may act to maximize its proximity from a predator with its fastest swimming possible.
₂₈₁ Even a larval fish may attain speeds in excess of 50 lengths s⁻¹ during a fast start (Müller
₂₈₂ and van Leeuwen, 2004). Therefore, prey may compensate for their smaller size and swim
₂₈₃ faster than a predator if the predator brakes for suction feeding (Fig. 3).

₂₈₄ When a prey swims faster than a predator, escape may be equally successful in a variety
₂₈₅ of directions (Eqn. 11). Any escape in this domain prohibits the predator from getting any

286 closer than the distance at which the prey initiates its escape (Fig. 3). Therefore, no trade-off
287 exists in this domain between predictability and evasiveness (Humphries and Driver, 1970).
288 This strategic benefits of this domain are compatible with our thinking about the motor
289 control of the escape response. We found that zebrafish larvae respond to a robotic predator
290 with directionality that is no more specific than moving away from the side of the body
291 exposed to a faster flow stimulus (Stewart et al., 2014). Such crude decision-making may be
292 achieved with a brief latency through relatively few synapses between the lateral line system
293 and escape circuit (Liu and Fethcho, 1999). The present results suggest that there is little
294 strategic disadvantage to this motor control. A short latency allows the prey to respond at
295 a relatively great distance and the coarse directional control yields an evasive response, even
296 for the fastest predators (Fig. 3C).

297 Different strategic dynamics come into play when the predator is faster than the prey.
298 At intermediate speeds ($1 < K < 10$), deviation from optimal strategy has the potential
299 for large adverse consequences (Fig. 2B, 4A–B) and it is therefore in this domain that
300 optimal strategy is most likely to be meaningful . To move in the optimal direction, the prey
301 must detect the heading and speed of the predator, which is likely to be achieved by the
302 visual or lateral line systems (Stewart et al., 2013; Dill, 1974; Paglianti and Domenici, 2006;
303 Higgs and Fuiman, 1996). It is additionally necessary that the motor system be capable of
304 rapidly propelling the fish in the optimal direction. As noted by Domenici, constraints on
305 these systems can prohibit a prey from conforming to an optimum (Domenici and Blagburn,
306 2011).

307 Sensory-motor constraints may play a role in guppies (*Poecilia reticulata*) that are preyed
308 upon by pike cichlids (*Crenicichla alta*) (Walker et al., 2005). These predators are approx-

309 imately twice as fast as the prey and the prey escape in a variety of directions. Survivor-
310 ship was found to be higher in prey that escaped directed directly away from predators
311 ($\alpha \sim 0^\circ$) than those which responded near the optimal direction that our model would pre-
312 dict ($\alpha_{\text{opt}} = 60.0^\circ$). It is possible that unsteady locomotion may account for this discrepancy.
313 The present model approximates the kinematics of predator and prey as a constant velocity,
314 whereas the escape response of the prey and acceleration during the strike may introduce
315 dynamics that would alter the predictions of a model.

316 The accuracy of a predator's strike is predicted to become a dominant factor in the
317 outcome when predators are much faster than the prey ($K > 10$). In this domain, differences
318 in minimum distance amount to minor performance differences across a broad range of escape
319 angles (Fig. 2B). Therefore, a predator fish gains a strategic advantage to strike at a higher
320 velocity for prey that move more quickly. This was observed by Wainwright *et al.*, who found
321 that cichlid predators strike at a faster speed when feeding on guppies (*Poecilia reticulata*)
322 than when feeding on smaller and slower zooplankton (*Artemia* sp.) (Wainwright *et al.*,
323 2001). We would further predict that successful evasion in faster approaches is correlated
324 with inaccuracy in the predator's strike.

325 Pursuit-evasion models offer a basis for studying the role of locomotion in predator-prey
326 interactions. The present model expands on Weihs and Webb (1984b), but retains most of
327 its key assumptions. Experimental tests of these assumptions could provide opportunities to
328 refine the theory and explore the sensory-motor coupling between predators and prey. Al-
329 though the present findings have the potential to inform our interpretations of the literature
330 , predator-prey experiments are rarely designed to test theory. For example, the behavior
331 of predator and prey fish are seldom studied simultaneously and the swimming speeds of

³³² both are often unreported. Studies that include these measurements most often do not mea-
³³³ sure the direction of a prey's escape. Therefore, many opportunities exist to expand our
³³⁴ understanding in this area.

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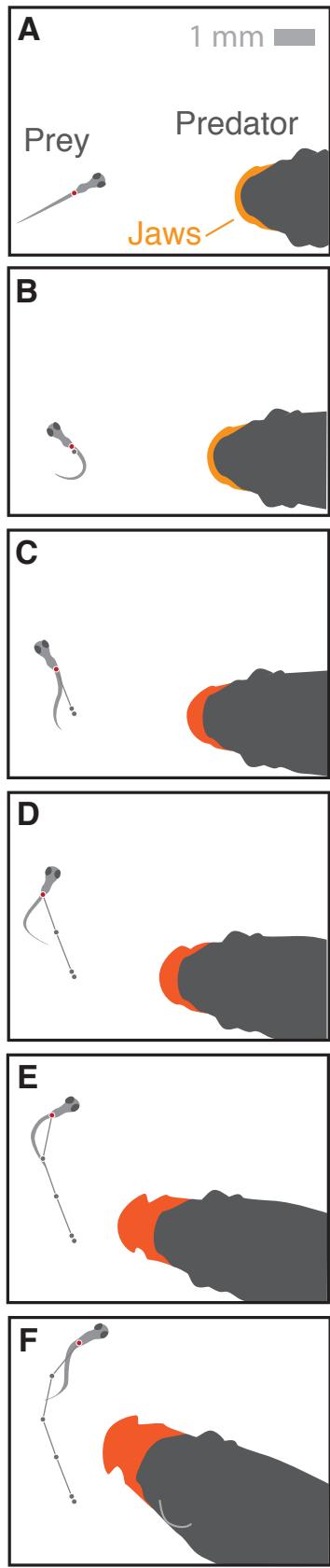


Figure 1: A predator-prey interaction in zebrafish. Silhouettes of zebrafish from a dorsal perspective have been traced from video stills (5 ms interval) as an adult attempts to capture a larva with a suction feeding strike. (A–B) On the predator's approach, the prey initiates a 'fast-start' escape response to accelerate away from the predator. The strike has yet to begin, as shown by the lack of protrusion by the jaws of the predator (orange). (C–D) The predator initiates a strike, which is visible from jaw protrusion (red). (E–F) With its jaws fully extended, the predator fails to capture the prey which proceeds to move away from the predator with rapid undulatory swimming. Recording from Stewart et al. (2014).

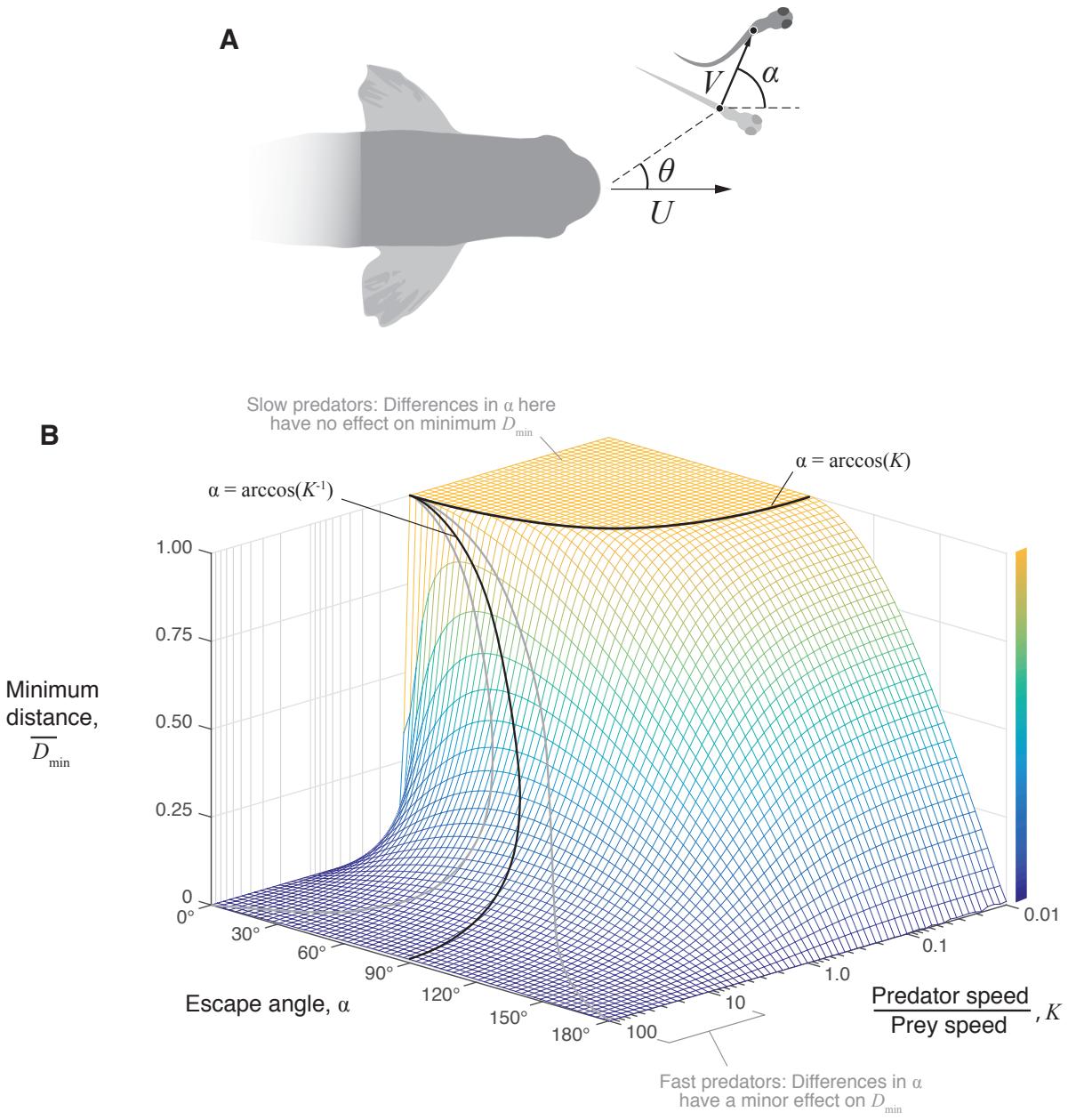


Figure 2: **A pursuit–evasion model for predator–prey interactions in fish.** (A) Pursuit–evasion models consider the motion of a predator (viewed from dorsal perspective) with speed U and a prey with speed V and escape angle α . Some versions of this model consider prey positioned lateral to the predator’s approach ($\theta_0 > 0$). (B) Numerical simulations were run at varying escape angle and predator approach speed (with $\theta_0 = 0$) to examine variation in the minimum distance. At $K > 1$, the optimal angle (black curve) was predicted analytically (Eqn. refK_j1 by Weihs and Webb (1984a)). Deviation from the optimum by $0.1\overline{D}_{\min}$ (gray curves) is shown to increase at greater values of K . The performance plateau where $D_{\min} = 1$ is predicted by Eqn.7.

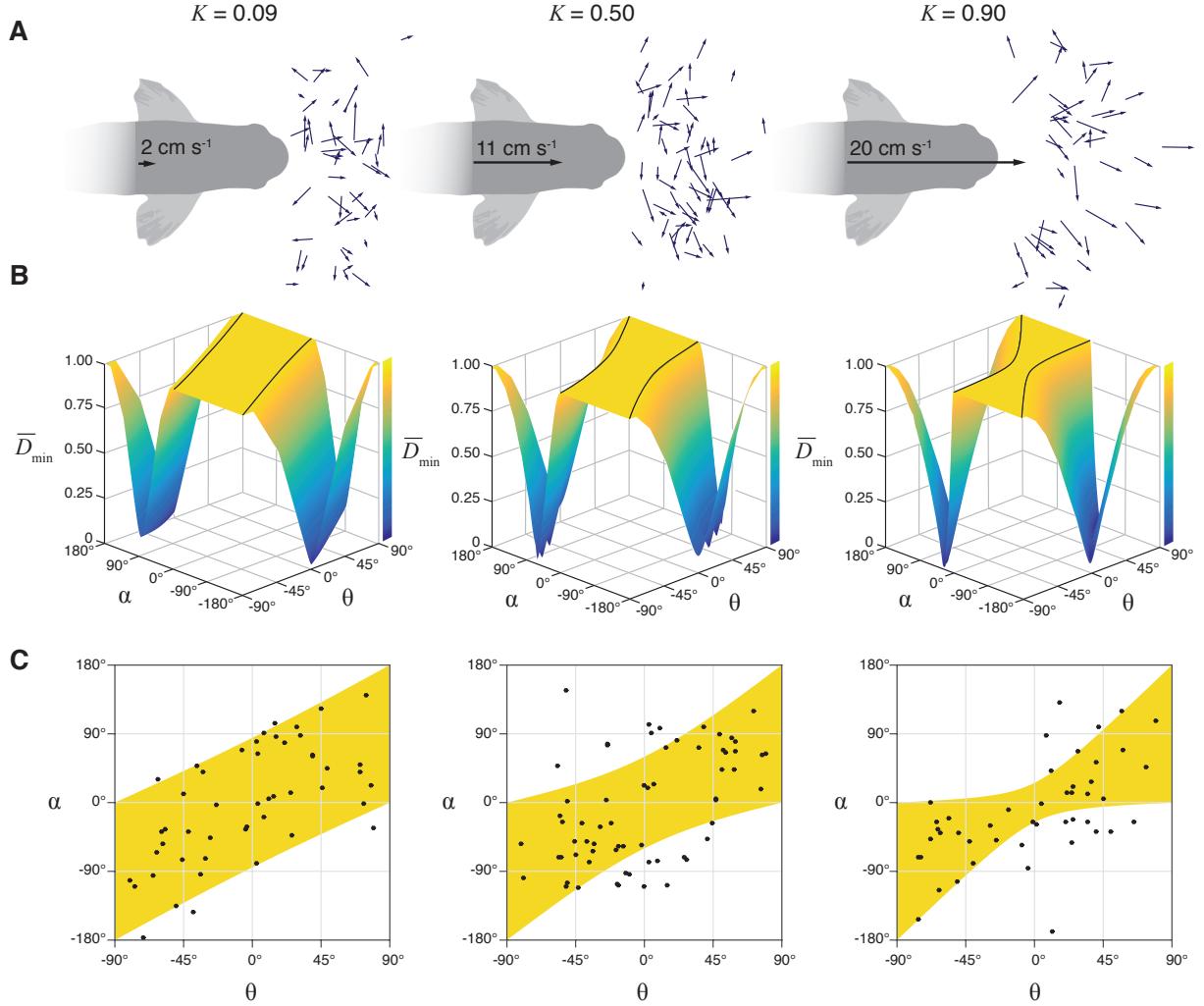


Figure 3: Model predictions and measurements of the fast start. The pursuit–evasion model was compared with experiments that recorded the responses of larval zebrafish that were approached by a robotic predator at three speeds ($2, 11$ and 20 cm s^{-1}) (Stewart et al., 2014). The results of experiments and modeling are arranged in column that correspond to each of these speeds. **(A)** The fast–start responses are illustrated by the center–of–body displacement for the two stages of the behavior (blue arrow). **(B)** Numerical results of the simulated interactions show how the minimum distance (\overline{D}_{\min}) varies with the escape angle(α) and initial position (θ_0). The plateau region (defined by Eqn. 7) shows an area where $\overline{D}_{\min} = 1$. **(C)** This area (in yellow) is plotted with measurements of the initial position and escape angle of the measured responses shown in **A**.

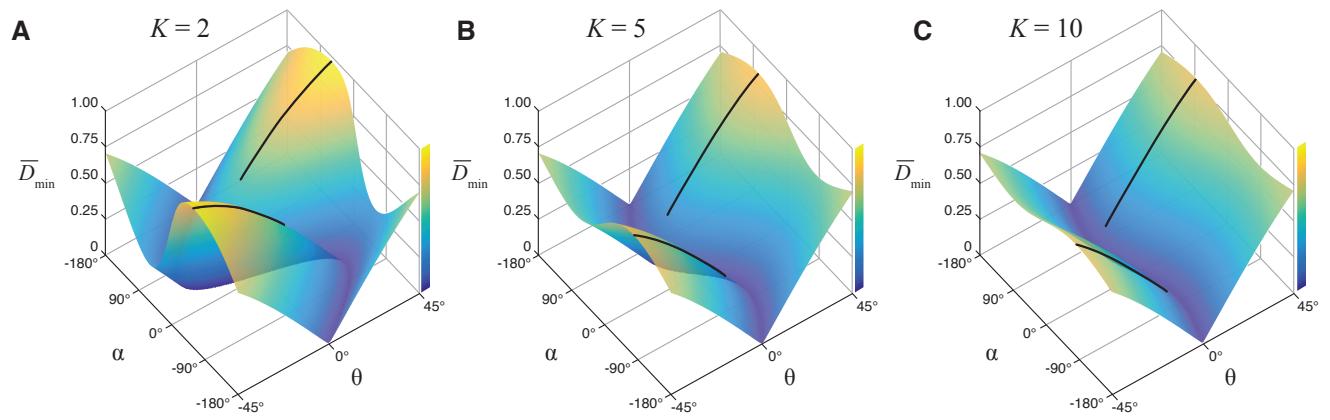


Figure 4: Evasive performance when the predator is faster than the prey. Numerical simulations calculated the minimum distance for variable initial position (θ_0) and escape angle (α) of the prey for predators that are faster than the prey by a factor of two (A), five (B), and ten (C).