Escape direction does not matter for some fish prey

Alberto Soto, William J. Stewart and Matthew J. McHenry

Department of Ecology & Evolutionary Biology,

University of California, Irvine

February 12, 2015

Abstract

Piscivorous interactions are commonly studied with an interest in the optimal strategy of prey to evade predators. However, it is unclear when the optimal strategy is meaningful to prey survival. Here we examine the theoretical consequences of deviation from optimal strategy for predators that approach at different speeds. With a focus on the minimum distance between predator and prey, we simulated these interactions with numerical and analytical mathematics and compared our predictions with measurements in zebrafish (*Danio rerio*). We found that differences in escape direction had only a small effect on the minimum distance when predators were more than an order of magnitude faster than the prey. Differences in direction had no effect on performance for a broad range of escape angles when the prey were faster than the predator, which is the case for zebrafish. Therefore, the escape angle either has no optimum or has a minor effect on predator-prey interactions in many situations where the predator is either slower or much faster than the prey. Optimal strategy is therefore most meaningful when prey are approached by a predator of intermediate speed. It remains to be seen whether prey behave optimally in this domain or whether optimal responses enhance survivorship.

1 Introduction

Biologists have long–appreciated the importance of predation in the ecology and evolution of prey species. This subject is extensive enough to fill the pages of books with the fascinating diversity of strategies that prey use to avoid encounters with predators (e.g. Ruxton et al., 2004) or to defend themselves when discovered (e.g. Emlen, 2014; Evans and Schmidt, 1990). In contrast, our understanding for how prey evade capture by locomotion is relatively rudimentary. Although biomechanical studies commonly speculate on the importance of locomotor performance to survival, relatively few have tested what aspects of locomotion are most meaningful in these interactions. Studies that have explored this subject (reviewed by Domenici and Blagburn, 2011) underscore the common-sense notion that the direction of an escape matters to a prey's survival. This idea is formalized by pursuit models that aim to determine the optimal direction of an escape response. The present study examined such a model (Weihs and Webb, 1984) to consider the strategic consequences of deviating from optimal strategy in piscivorous interactions. We compare the predictions of this model to experimental results in zebrafish (*Danio rerio*) (Stewart et al., 2014) and offer new interpretations of theory on prey strategy.

Pursuit models are an area of game theory that offers a basis for examining locomotor behavior in strategic terms. There is recent interest in revisiting these models (e.g. Howland, 1974; Weihs and Webb, 1984) with experimental studies that consider the behavior of both predators and prey. This includes work on running vertebrates (e.g. Wilson et al., 2013), birds (e.g. Hedenström and Rosén, 2001; Kullberg et al., 1998) and bats (e.g. Ghose et al., 2006) in flight, running insects (Domenici et al., 2008), flying insects (e.g. Combes et al.,

2012), and swimming zooplankton (e.g. Arnott et al., 1999; Heuch et al., 2007) and fishes (e.g. Domenici et al., 2000). These efforts offer the potential to reveal how sensory and motor systems govern the outcome of predator–prey interactions.

A piscivorous interaction offers some advantages as a model for examining the sensory-motor basis of predator evasion. In many cases, this interaction can be easily studied in a laboratory. Under artificial conditions, predatory fishes attempt to feed on prey and prey initiate a 'fast-start' escape response (Fig. 1). Both players operate with motion that is largely two-dimensional and therefore relatively simple to measure and describe. Zebrafish exhibit both predator evasion and predatory behavior in the lab (Stewart et al., 2013) and this species offers a growing wealth of understanding in physiology and neuroscience (e.g. McLean and Fetcho, 2011; Briggs, 2002) that may be leveraged for mechanistic insight on predator–prey interactions. In addition, fish offer one of the few biological pursuit systems that have been mathematically modeled (Weihs and Webb, 1984). This model offers specific predictions of swimming trajectories that may be tested with kinematic measurements.

Deviation from optimal strategy has commonly been interpreted as a strategic adaptation. The protean hypothesis suggests that prey which are unpredictable should have an advantage in predator evasion over predictable prey (Humphries and Driver, 1970). This idea may apply to the erratic motion of an individual or to predators that learn or adapt to the behavior of a population of prey that exhibits variable motion. The 'fast start' escape response of fish generates a turn and acceleration of the body in a particular direction and therefore would appear to correspond to the latter category (Weihs, 1973), although a sequence of fast starts could offer the opportunity for erratic motion. Nonetheless, a potential trade-off exists for the direction of a fast start between optimal displacement away from an advancing predator

4

and the benefit of being unpredictable.

Interpretations of prey motion have generally not considered the effect of deviating from optimal strategy. For example, it is not clear whether an escape that is 5° or 50° from the optimum predicted by Weihs and Webb (1984) has a major or negligible effect on evasion success. If evasive performance is insensitive to differences in escape direction, then no trade-off exists between evasiveness and predictability. In short, it is unclear when optimal strategy matters. The present study therefore revisited the mathematics of the Weihs and Webb (1984) model to examine how deviation from optimal strategy affects prey evasion. We expanded this model and performed numerical simulations for comparison with experimental results. In this effort, we arrived at new interpretations of theory on prey evasion. In particular, we identified conditions where the escape direction is predicted to have little or no effect on the evasiveness of prey.

2   Optimal prey strategy

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

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

88 consequences of playing with a particular strategy (Webb, 2007). For pursuit models, the

89 payoff is often defined as the minimum distance between predator and prey. This quantity

90 reflects the condition where the predator has the best opportunity to capture the prey. The

91 optimal strategy for an evasive prey is therefore defined as the escape angle that yields the

92 greatest minimum distance (Weihs and Webb, 1984).

93 Predicting the distance between predator and prey requires relatively few parameters

94 under some simplifying assumptions. In the rapid events of a predatory strike, it is reasonable

95 to approximate the predator's motion as a constant speed, U. If one neglects the acceleration

96 period of the fast start, then the prey's motion may be approximated with a constant speed,

97 V, at an escape angle α, defined with respect to the heading of the predator (Fig. 1A).

98 Under these conditions, the distance between predator and prey, D, may be calculated over

99 time:

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

100 where X_0 is the starting position of the prey.

101 The minimum distance, the payoff in this game, may be calculated from the distance

102 equation. The first step is to calculate the time, $t_{\min}$, at which the minimum distance

103 occurs. This may be found from the root of the first derivative of Eqn. 1 with respect to

104 time, which yields the following solution:

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

105 where K indicates the speed of the predator relative to the prey ($K = U/V$). Weihs and

106 Webb observed that this equation yields negative values of time where $K < 1$ and is therefore

6

only useful when the predator is faster than the prey (Weihs and Webb, 1984). The minimum distance was consequently determined for $K > 1$ by solving for distance (Eqn. 1) at $t_{\min}$:

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

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

Finally, the optimal strategy for the prey may be determined by finding the escape angle that yields the greatest minimum distance. This occurs where the derivative of Eqn. 3 with respect to α is equal to zero, which is explicitly described by the following equation:

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

Among the solutions that satisfy this equation, Weihs and Webb proposed that the following indicates the optimal strategy when the predator is faster than the prey ($K > 1$):

$$\alpha_{\mathrm{opt}} = \pm \arccos K^{-1}.\tag{5}$$

We added the $\pm$ symbol to this expression to indicate that prey are equally effective if escaping at an optimal angle toward the left ($\alpha > 0$), or right ($\alpha < 0$) of the predator's heading. For relatively fast prey ($K \leq 1$), Weihs and Webb suggested that the optimal solution consists of swimming directly away from the predator ($\alpha = 0$) (Weihs and Webb, 1984). Therefore, for any predator speed, this model offers predictions for how a prey can direct its escape to maximize its chances for survival by creating the greatest distance from a predator.

3 When optimal strategy matters

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

Our results suggest that the fast start is unlikely to be effective at any escape angle when a prey is approached by a very fast predator. For example, if a predator is an order of magnitude faster than its prey (i.e. $K = 10$), then the prey can do no better than

8

displace its body by 10% of its initial distance from the predator (Fig. 2B). In addition,

differences in escape angle have little effect on the minimum distance. An escape that is

24.5° larger or smaller than the optimum yields a minimum distance that is less than the

value at the optimum by 0.1 (i.e. 1% of the starting position of the prey). These metrics

become increasingly unfavorable for the prey when approached by an even faster predator

(Fig. 2B). At these speeds, inaccuracy in the feeding strike is likely a more decisive factor

to prey survival than anything the prey may do in response.

A different picture emerges when one considers prey that move more quickly than their

predators (i.e. $K < 1$). This condition occurs when predators brake or glide slowly on their

approach toward a prey (Higham, 2007; Higham et al., 2005) while the prey initiates a rapid

escape. For a variety of escape angles, the fast start of these prey cause the predator to

reach no closer than the starting distance (i.e. $\overline{D}_{\min} = 1$, Fig. 2B). In order to define the

bounds of this domain, it is useful to consider the first derivative of the distance function

with respect to time:

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

A prey achieves an optimal escape ($\overline{D}_{\min} = 1$) when the distance function only increases

as a function of time (i.e. $\frac{\partial D^2}{\partial t} \geq 0$). This holds true for $\alpha = 0$, which Weihs and Webb

proposed as the optimal direction (Weihs and Webb, 1984). However, it also holds true

that distance increases for another solution to Eqn. 4 ($\alpha = \pm \arccos K$) and all values in

between. Therefore, the following defines the domain of optimal directions when the prey is

faster than the predator ($K < 1$):

$$-\arccos(K) \leq \alpha \leq \arccos(K). \tag{7}$$

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

165 approach speed of the predator, then a wide range of angles yield equally successful escapes

166 for the prey and thereby define a performance plateau.

167 The domain where optimal the optimal strategy matters the most resides between where

168 the prey and predator are equivalent in speed and where the predator is an order of mag-

169 nitude faster ($1 < K < 10$). In this domain, prey are capable of attaining appreciable

170 minimum distance values and there is a penalty for deviating from the optimal angle (Fig.

171 2B). Therefore, a prey fish has an incentive to conform to the optimal prediction when

172 encountering a slightly faster predator.

4   Comparing models with measurements

174 We were interested in examining whether optimal strategy matters under experimental con-

175 ditions. This was addressed with recent measurements on larval zebrafish, which are preyed

176 upon by adults of the same species (Stewart et al., 2013). This work included experiments

177 that used a robot to simulate the approach of a predator toward prey in the dark, with

178 recordings of the position at which the prey responded with a fast start and the direction of

179 that response (Stewart et al., 2014). This evasive action was stimulated by the lateral line

180 system of the prey, which detected the water flow generated by the approaching predator.

181 As detailed above, the predictions of the model depend on the speed of the predator

182 relative to the prey. The approach speed of the robot, and consequently K, was varied to

183 span the range of values observed for a live predator (Stewart et al., 2013). Our calculations

184 of K used a prey speed ($U = 22$ cm s^{-1}) from the literature that approximates the maximum

185 value attained during a fast start for larvae of this species (Budick and O'Malley, 2000; Müller

186 and van Leeuwen, 2004). As a consequence of the relatively slow approach made by these

187 suction-feeding predators, the prey had the potential to move faster at all approach speeds,

188 which yielded K-values that were uniformly less than unity (Fig. 3A).

189   One discrepancy between the model and our experiments was that the majority of prey

190 fish did not exhibit an initial position that was aligned with the heading of the predator

191 robot. This condition has biological relevance because it corresponds to a situation where

192 a predator fails to approach with a prey with perfect accuracy. We therefore modified the

193 Weihs and Webb model by adding a lateral component to the initial position of the prey in

194 our distance function. However, we followed the same procedure (as in Eqns. 2–3) to arrive

195 at a minimum distance function (see Supplemental Materials for details). We found that

196 our solutions were was simplified by the use of polar coordinates. For example, we found the

197 following equation for the minimum distance:

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

198 where R_0 and θ_0 are the initial radial and angular positions of the prey relative to the mouth

199 of the predator (Fig. 2A). Numerical solutions to this equation show a broad range of angular

200 positions and escape angles that define a performance plateau where $D_{\min} = 1$ (Fig. 3B). We

201 found the margins of this plateau using a similar procedure as outlined above. Specifically,

202 we solved for the conditions where the derivative of the minimum distance with respect to

203 α was equal to zero:

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

204 We found the solutions that satisfy this equation by setting the terms in the numerator

equal to zero. The solution for $K > 1$ was similar to Eqn. 5, though the angular position determines the sign of the optimal angle:

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

(10)

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

$$0 \leq \alpha \geq \theta_0 - \arccos(K \cos\theta_0)) \text{ if } \theta_0 < 0,$$

(11)

$$0 \leq \alpha \leq \theta_0 + \arccos(K \cos\theta_0)) \text{ if } \theta_0 > 0$$

(12)

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

Using this formulation of the pursuit model, we evaluated how the measured responses of prey compared to the model predictions (Fig. 3C). This comparison revealed that the vast majority of larvae responded at a position and with an escape direction that was predicted to yield maximal performance ($\overline{D}_{\mathrm{min}} = 1$). This was true even at the fastest predator approach speed, where a larger number of individuals responded outside of the plateau. According to

12

the model's predictions, the large variation in observed escape direction incurs no penalty in the evasive performance of most larvae.

5 ???

6 Predator strategy

Although the present pursuit models were formulated with a focus on prey fish, they provide the opportunity to consider the strategy of fish predators. It first merits pointing out that the payout considered presently is normalized by the initial response distance of the prey (Figs. 2–3). Therefore, the absolute distance traversed by a prey is predicted to be proportional to the initial response distance. The predator may act to minimize this distance with a slower approach, which will serve to reduce the stimulus intensity for the visual (CITE) and lateral line (CITE) systems. This is one benefit to the braking behavior that suction-feeding predators exhibit before a strike (Higham, 2007; Higham et al., 2005). Another potential benefit to a slow approach is greater accuracy in the timing and direction of a suction-feeding strike, which is restricted to a brief duration over a relatively small region around a predator's mouth.

Our results indicate some of the strategic advantages for predators to approach prey relatively quickly. Moving faster than the escaping prey can greatly diminish the escape angles that are beneficial for evasion (Fig. 2B). As we discussed above ("Optimal prey strategy"), the fast start can become ineffective at offering any benefit to predator evasion when the predator is substantially faster than the prey and headed directly at the prey. Such

13

₂₄₃ a high-speed approach may present a challenge for a predator to coordinate the timing of

₂₄₄ the strike (Higham, 2007; Higham et al., 2005), but we have also found that it offers some

₂₄₅ advantages to the evasiveness of the prey.

₂₄₆ We conducted a series of simulations that examine the effect of an inaccurate strike by

₂₄₇ a fast predator. As in the simulations we used to compare with experimental results, we

₂₄₈ calculated the minimum distance for a range of values in escape angle and initial angular

₂₄₉ position. If we assume that predator fish lack the interception targeting used by bats Ghose

₂₅₀ et al. (2006) and birds Kane and Zamani (2014), we may interpret deviation from a zero

₂₅₁ angular position as an indication of strike inaccuracy by the predator.

₂₅₂ The model's assumptions could be violated by the system. For example, a prey fish

₂₅₃ cannot move in an optimal direction that maximizes its distance from a predator if it cannot

₂₅₄ detect the predator's speed (Weihs and Webb, 1984).

References

Arnott, S. A., Neil, D. M. and Ansell, A. D. (1999). Escape trajectories of the brown shrimp *Crangon crangon*, and a theoretical consideration of initial escape angles from predators .

Briggs, J. P. (2002). The zebrafish: A new model organism for integrative physiology. *Am. J. Physiol. Regulatory Integrative Comp. Physiol* **282**, R3–R9.

Budick, S. A. and O'Malley, D. M. (2000). Locomotor repertoire of the larval zebrafish: Swimming, turning and prey capture. *J. Exp. Biol.* **203**, 2565–2579.

Combes, S. A., Rundle, D. E., Iwasaki, J. M. and Crall, J. D. (2012). Linking biomechanics and ecology through predator–prey interactions: flight performance of dragonflies and their prey. *J. Exp. Biol.* **215**, 903–913.

Domenici, P., Batty, R. S., Simila, T. and Ogam, E. (2000). Killer whales (*Orcinus orca*) feeding on schooling herring (*Clupea harengus*) using underwater tail-slaps: kinematic analyses of field observations. *J. Exp. Biol* **203**, 283–294.

Domenici, P. and Blagburn, J. M. (2011). Animal escapology I: theoretical issues and emerging trends in escape trajectories. *J. Exp. Biol.* **214**, 2463–2473.

Domenici, P., Booth, D., Blagburn, J. M. and Bacon, J. P. (2008). Cockroaches keep predators guessing by using preferred escape trajectories. *Curr. Biol.* **18**, 1792–1796.

Emlen, D. J. (2014). *Animal Weapons:The Evolution of Battle*. New York: Macmillan.

15

Evans, D. L. and Schmidt, J. O. (1990). *Insect Defenses: Adaptive Mechanisms and Strategies of Prey and Predators.* Albany, NY: SUNY Press.

Ghose, K., Horiuchi, T. K., Krishnaprasad, P. S. and Moss, C. F. (2006). Echolocating Bats Use a Nearly Time-Optimal Strategy to Intercept Prey. *PLoS biology* **4**, e108.

Hedenström, A. and Rosén, M. (2001). Predator versus prey: on aerial hunting and escape strategies in birds. *Behavioral Ecology* **12**, 150–156.

Heuch, P. A., Doall, M. H. and Yen, J. (2007). Water flow around a fish mimic attracts a parasitic and deters a planktonic copepod. *Journal Of Plankton Research* **29**, i3–i16.

Higham, T. E. (2007). Feeding, fins and braking maneuvers: locomotion during prey capture in centrarchid fishes. *J. Exp. Biol* **210**, 107–117.

Higham, T. E., Malas, B., Jayne, B. C. and Lauder, G. V. (2005). Constraints on starting and stopping: behavior compensates for reduced pectoral fin area during braking of the bluegill sunfish *Lepomis macrochirus*. *J. Exp. Biol* **208**, 4735–4746.

Howland, H. C. (1974). Optimal strategies for predator avoidance: The relative importance of speed and manoeuvrability. *J. Theor. Biol.* **47**, 333–350.

Humphries, D. A. and Driver, P. M. (1970). Protean defence by prey animals. *Oecologia* **5**, 285–302.

Isaacs, R. (1965). *Differential Games: A Mathematical Theory with Applications to Warfare and Pursuit, Control and Optimization.* New York: John Wiley and Sons, Inc.

Kane, S. A. and Zamani, M. (2014). Falcons pursue prey using visual motion cues: new perspectives from animal-borne cameras. *J. Exp. Biol* **217**, 225–234.

Kullberg, C., Jakobsson, S. and Fransson, T. (1998). Predator-induced take-off strategy in great tits (Parus major). *Proceedings of the Royal Society of London. Series B: Biological Sciences* **265**, 1659–1664.

McLean, D. L. and Fetcho, J. R. (2011). Movement, technology and discovery in the zebrafish. *Curr. Opin. Neurobiol.* **21**, 110–115.

Müller, U. K. and van Leeuwen, J. L. (2004). Swimming of larval zebrafish: ontogeny of body waves and implications for locomotory development. *J. Exp. Biol* **207**, 853–868.

Ruxton, G. D., Sherratt, T. N. and Speed, M. (2004). *Avoiding Attack:The Evolutionary Ecology of Crypsis, Warning Signals and Mimicry.* Oxford: OUP Oxford.

Stewart, W. J., Cardenas, G. S. and McHenry, M. J. (2013). Zebrafish larvae evade predators by sensing water flow. *J. Exp. Biol.* **216**, 388–398.

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

Webb, J. N. (2007). *Game Theory: Decisions, Interaction and Evolution.* London: Springer.

Weihs, D. (1973). The mechanism of rapid starting of slender fish. *Biorheology* **10**, 343–350.

Weihs, D. and Webb, P. W. (1984). Optimal avoidance and evasion tactics in predator-prey interactions. *J. Theor. Biol.* **106**, 189–206.

314 **Wilson, A. M., Lowe, J. C., Roskilly, K., Hudson, P. E., Golabek, K. A. and**

315 **McNutt, J. W.** (2013). Locomotion dynamics of hunting in wild cheetahs. *Nature* **498**,
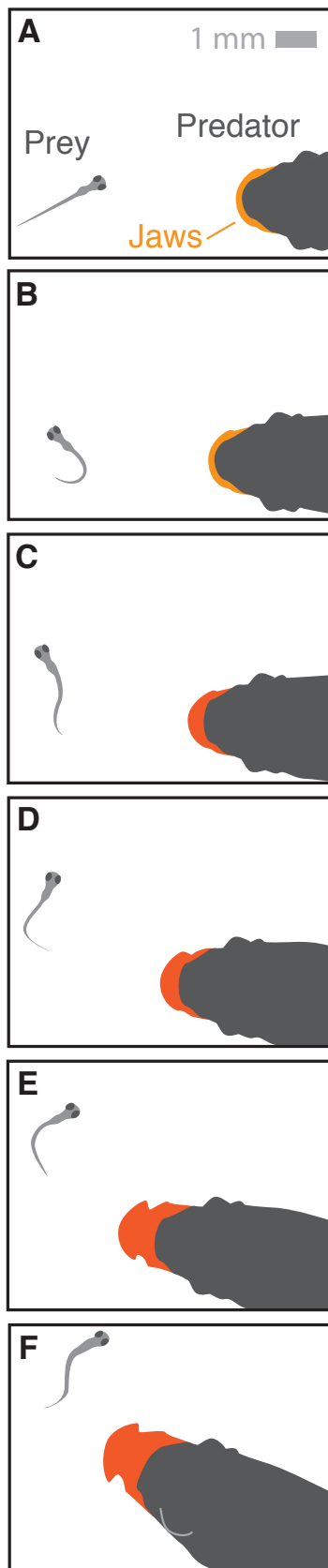
316 185–189.

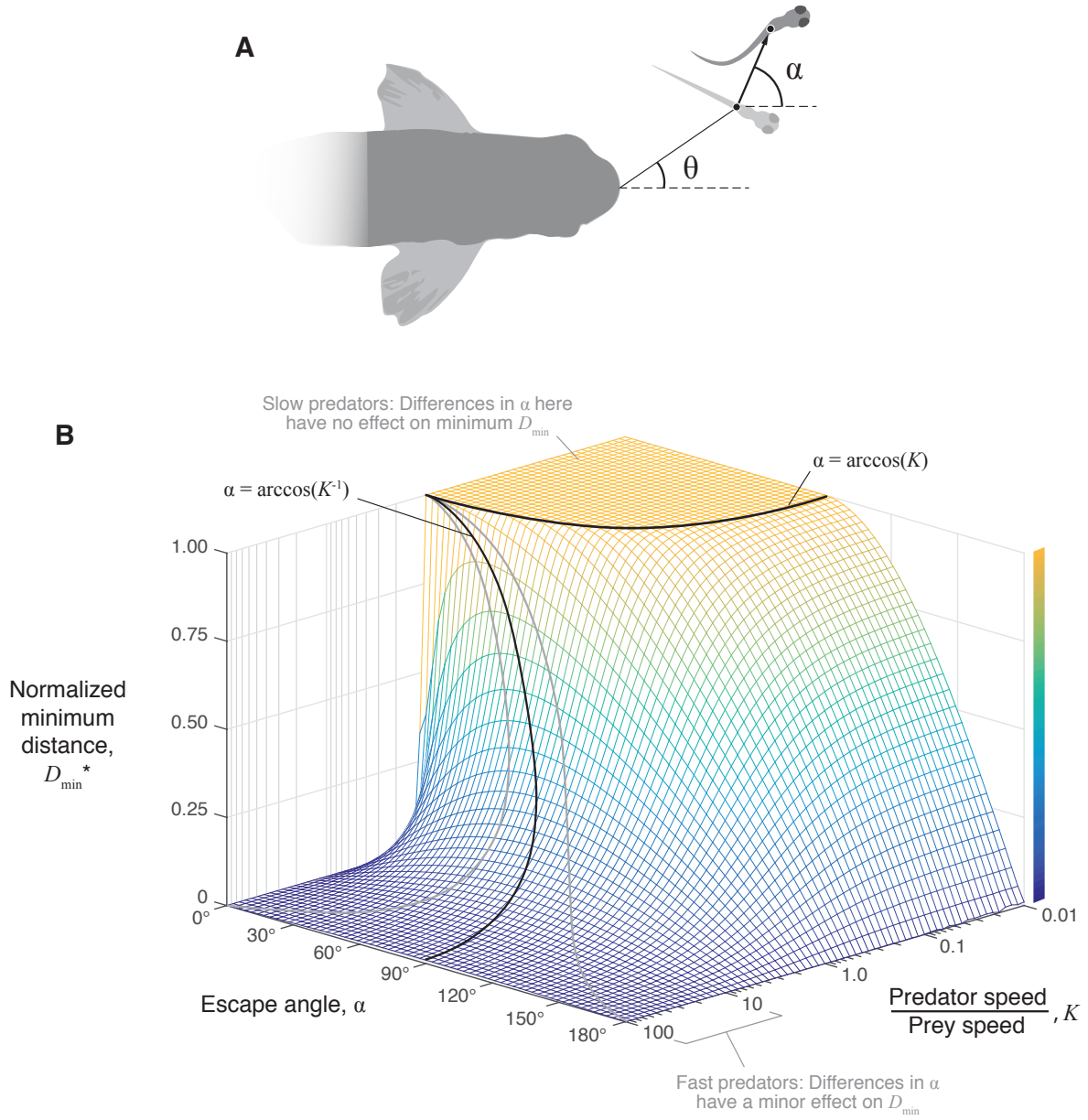Figure 1: **A predator-prey interaction in zebrafish. (A)**

Figure 2: **The Homicidal Chauffeur model, applied to prey strategy. (A)** Simulations predict the direction of a prey's fast start relative to initial position and velocity of a predator. **(B)** Numerical simulations were run at varying escape angle and predator approach speed to examine variation in the minimum distance. At $K > 1$, the optimal angle.
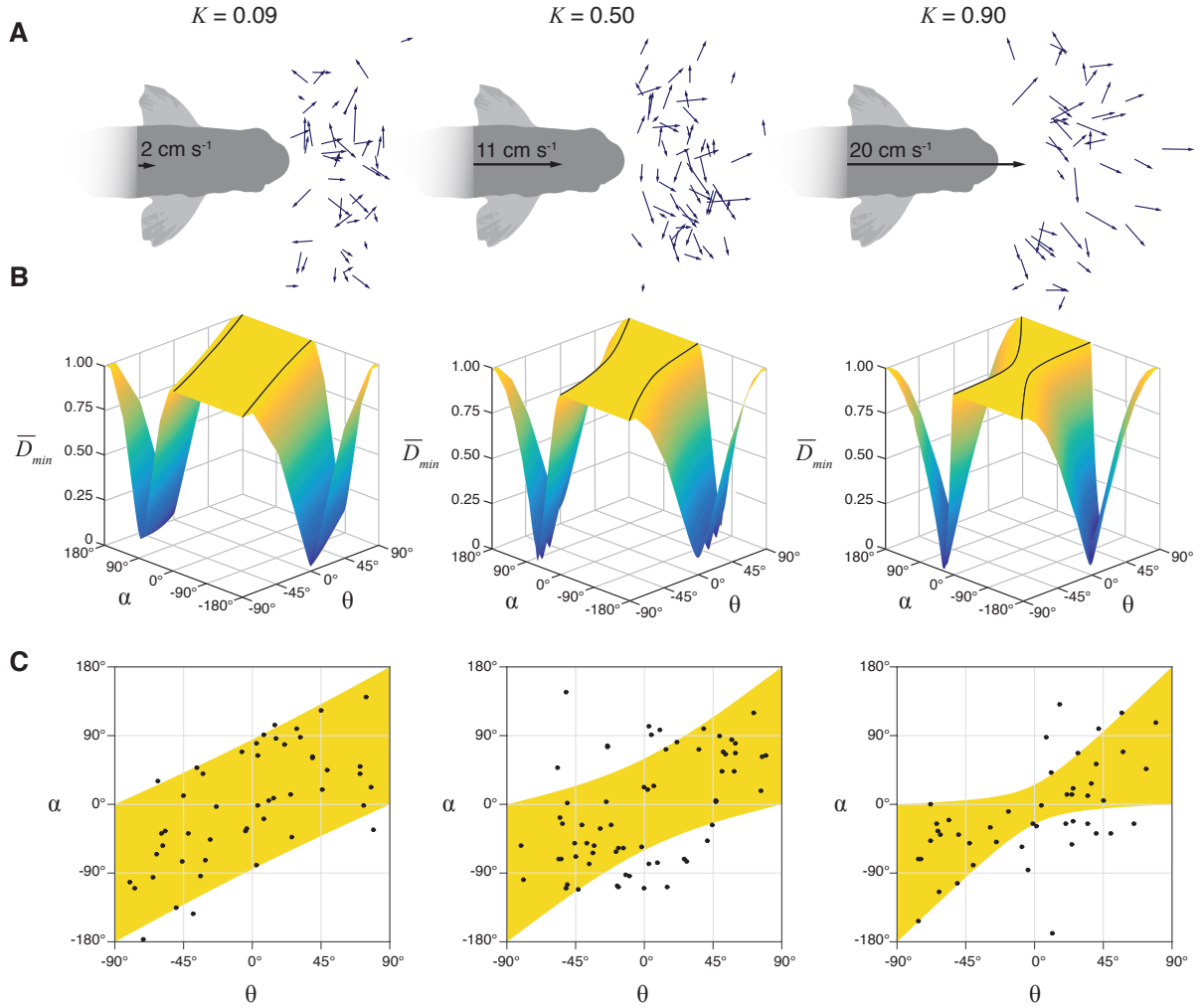. .

Figure 3: **Model predictions and measurements of the fast start. (A)**

Figure 4: **Model predictions and measurements of the fast start. (A)**