

<sup>1</sup> Escape direction does not matter for some fish prey

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## Abstract

5 Predator-prey interactions are commonly studied with an interest in determining  
6 whether prey adopt an optimal strategy to evade predators. However, the benefits  
7 of an optimal strategy are often unclear and adopting such behavior may incur costs  
8 to the prey. Here we examine the theoretical consequences of deviating from optimal  
9 strategy in fish that are preyed upon by fish predators. We simulated these interac-  
10 tions with numerical and analytical mathematics and compared our predictions with  
11 measurements in zebrafish (*Danio rerio*). As in previous models, we focused on the  
12 effect of the escape direction on the minimum distance between predator and prey.  
13 We found that differences in escape direction had only a small effect on the minimum  
14 distance when predators were more than an order of magnitude faster than the prey.  
15 Furthermore, differences in direction had no effect on performance for a broad range  
16 of escape angles when the prey were faster than the predator, which is the case for ze-  
17 brafish. Optimal strategy is therefore most meaningful to these prey when approached  
18 by a predator of intermediate speed. When the predator is either slower or much faster  
19 than the prey, optimal strategy may not exist or offer little benefit to predator evasion.

## 20 1 Introduction

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

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

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

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

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

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

## 76 **2 Optimal prey strategy**

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

85 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 acceleration period of the fast start, then the prey's motion may be approximated with a constant speed,  $V$ , at an escape angle  $\alpha$ , defined with respect to the heading of the predator (Fig. 1A). 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 for  $K < \cos \alpha$ , which is the case when the prey is faster than the predator and  $0 \leq \alpha \leq \pi/2$ . The minimum distance was consequently determined for

<sup>106</sup>  $K > 1$  by solving for distance (Eqn. 1) at  $t_{\min}$ :

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

<sup>107</sup> where  $\overline{D}_{\min}^2$  is the minimum distance normalized by the starting position of the prey.

<sup>108</sup> Finally, the optimal strategy for the prey may be determined by finding the escape angle  
<sup>109</sup> that yields the greatest minimum distance. This occurs where the derivative of Eqn. 3 with  
<sup>110</sup> respect to  $\alpha$  is equal to zero, which is explicitly described by the following equation:

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

<sup>111</sup> Among the solutions that satisfy this equation, Weihs and Webb proposed that the following  
<sup>112</sup> indicates the optimal strategy when the predator is faster than the prey ( $K > 1$ ):

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

<sup>113</sup> We added the  $\pm$  symbol to this expression to indicate that prey are equally effective if  
<sup>114</sup> escaping at an optimal angle toward the left ( $\alpha > 0$ ), or right ( $\alpha < 0$ ) of the predator's  
<sup>115</sup> heading. For relatively fast prey ( $K \leq 1$ ), Weihs and Webb suggested that the optimal  
<sup>116</sup> solution consists of swimming directly away from the predator ( $\alpha = 0$ ) (Weihs and Webb,  
<sup>117</sup> 1984). Therefore, for any predator speed, this model offers predictions for how a prey can  
<sup>118</sup> direct its escape to maximize its chances for survival by creating the greatest distance from  
<sup>119</sup> a predator.

### <sup>120</sup> 3 When optimal strategy matters

<sup>121</sup> An optimum adopts a different meaning if it corresponds to a shallow peak in performance or  
<sup>122</sup> defines a local peak that is much smaller than the global maximum. We considered whether

123 these conditions exist in evasion strategy by calculating how the payoff in this pursuit model,  
124 the minimum distance (Weihs and Webb, 1984), varies with escape angle and the relative  
125 speed of the predator. This was considered by formulating a performance landscape of prey  
126 strategy. As an alternative to analytical mathematics (Eqn. 3), we first formulated this  
127 landscape with a numerical approach that is simple enough to execute in a spreadsheet,  
128 but which we implemented in Matlab (MathWorks, Natick, MA, USA). This was done by  
129 defining a series of time values at an equal interval, which was used to calculate the positions  
130 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  
131 minimum value of the distance between them was determined in this way for variable escape  
132 angle and predator speed, over a range of  $K$  and  $\alpha$  values (Fig. 2B). This yielded results that  
133 were coincident with the analytical equation for  $\bar{D}_{\min}$  formulated by Weihs and Webb (1984)  
134 for relatively fast predators ( $K > 1$ , Eqn. 3). However, the advantage of the numerical  
135 calculations was that they allowed us to examine variation in the minimum distance for  
136 slower predators (i.e.  $K < 1$ ) as well. The resulting performance landscape (Fig. 2B)  
137 illustrates how the minimum distance varies over a broad range of values in the relative  
138 speed of the predator and escape angle of the prey.

139 Our results suggest that the fast start is unlikely to be effective at any escape angle  
140 when a prey is approached by a very fast predator. For example, if a predator is an order  
141 of magnitude faster than its prey (i.e.  $K = 10$ ), then the prey can do no better than  
142 displace its body by 10% of its initial distance from the predator (Fig. 2B). In addition,  
143 differences in escape angle have little effect on the minimum distance. An escape that is  
144  $24.5^\circ$  larger or smaller than the optimum yields a minimum distance that is less than the  
145 value at the optimum by 0.1 (i.e. 1% of the starting position of the prey). These metrics

<sup>146</sup> become increasingly unfavorable for the prey when approached by an even faster predator  
<sup>147</sup> (Fig. 2B). At these speeds, inaccuracy in the feeding strike is likely a more decisive factor  
<sup>148</sup> to prey survival than anything the prey may do in response.

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

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

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

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

<sup>162</sup> This analysis suggests that if the escape response of a prey is capable of exceeding the  
<sup>163</sup> approach speed of the predator, then a wide range of angles yield equally successful escapes  
<sup>164</sup> for the prey and thereby define a performance plateau.

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

## <sub>171</sub> 4 Comparing models with measurements

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

<sub>179</sub> As detailed above, the predictions of the model depend on the speed of the predator  
<sub>180</sub> relative to the prey. The approach speed of the robot, and consequently  $K$ , was varied to  
<sub>181</sub> span the range of values observed for a live predator (Stewart et al., 2013). Our calculations  
<sub>182</sub> of  $K$  used a prey speed ( $U = 22 \text{ cm s}^{-1}$ ) from the literature that approximates the maximum  
<sub>183</sub> value attained during a fast start for larvae of this species (Budick and O’Malley, 2000; Müller  
<sub>184</sub> and van Leeuwen, 2004). As a consequence of the relatively slow approach made by these  
<sub>185</sub> suction-feeding predators, the prey had the potential to move faster at all approach speeds,

<sup>186</sup> which yielded  $K$ -values that were uniformly less than unity (Fig. 3A).

<sup>187</sup> One discrepancy between the model and our experiments was that the majority of prey  
<sup>188</sup> fish did not exhibit an initial position that was aligned with the heading of the predator  
<sup>189</sup> robot. This condition has biological relevance because it corresponds to a situation where  
<sup>190</sup> a predator fails to approach a prey with perfect accuracy. We therefore modified the Weihs  
<sup>191</sup> and Webb model by adding a lateral component to the initial position of the prey in our  
<sup>192</sup> distance function. However, we followed the same procedure (as in Eqns. 2–3) to arrive  
<sup>193</sup> at a minimum distance function (see Supplemental Materials for details). We found that  
<sup>194</sup> our solutions were simplified by the use of polar coordinates. For example, we found the  
<sup>195</sup> following equation for the minimum distance:

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

<sup>196</sup> where  $R_0$  and  $\theta_0$  are the initial radial and angular positions of the prey relative to the mouth  
<sup>197</sup> of the predator (Fig. 2A). Numerical solutions to this equation show a broad range of angular  
<sup>198</sup> positions and escape angles that define a performance plateau where  $D_{\min} = 1$  (Fig. 3B). We  
<sup>199</sup> found the margins of this plateau using a similar procedure as outlined above. Specifically,  
<sup>200</sup> we solved for the conditions where the derivative of the minimum distance with respect to  
<sup>201</sup>  $\alpha$  was equal to zero:

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

<sup>202</sup> We found the solutions that satisfy this equation by setting the terms in the numerator equal  
<sup>203</sup> to zero. The solution for  $K > 1$  and  $\theta_0 < \arccos(K^{-1})$  was similar to Eqn. 5, though the

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

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

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

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

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

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

222 **5 Predator strategy**

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

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

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

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

250 The results of these simulations illustrate the relative contribution of escape angle and  
251 strike accuracy on evasion for different approach speeds. For a predator that is twice as fast  
252 as the prey ( $K = 2$ ), the minimum distance varies substantially with both escape direction  
253 and strike accuracy (Fig. 4A). For example, the optimal escape angle ( $\alpha_{\text{opt}} = 60.0^\circ$ ) generates  
254 a minimum distance ( $\bar{D}_{\min} = 0.71$ ) that is more than two orders of magnitude better than  
255 what may be achieved with the least effective escape direction ( $\bar{D}_{\min} = 0.002$ ) when the  
256 prey is positioned  $15^\circ$  from the predator's heading. This advantage in minumum distance  
257 is not greatly reduced ( $\bar{D}_{\min} = 0.50$  at  $\alpha_{\text{opt}} = 60^\circ$ ) if the predator successfully aligns its  
258 strike ( $\theta_0 = 0^\circ$ ). However, the escape angle plays a reduced role in aiding predator evasion  
259 at faster approach speeds. For example, when the predator is 10-times faster (Fig. 4C)  
260 and inaccurate ( $\theta_0 = 15^\circ$ ), then the optimal escape angle ( $\alpha_{\text{opt}} = 84.3^\circ$ ) yields a minimum  
261 distance only slightly more than twice the value than the least effective angle ( $\bar{D}_{\min} = 0.35$   
262 versus  $\bar{D}_{\min} = 0.16$ ). Furthermore, the optimal escape angle is relatively ineffective for an  
263 accurate strike ( $\theta_0 = 0^\circ$ ) since the minimum distance is  $\bar{D}_{\min} = 0.10$ . Therefore, the accuracy  
264 of a predators' strike becomes an increasingly dominant factor in determining prey survival  
265 with predators that are many times faster than the prey.

<sub>266</sub> **6 Conclusions**

<sub>267</sub> The present results offer a new perspective on predator–prey strategy.

<sub>268</sub> The model’s assumptions could be violated by the system. For example, a prey fish  
<sub>269</sub> cannot move in an optimal direction that maximizes its distance from a predator if it cannot  
<sub>270</sub> detect the predator’s speed (Weihs and Webb, 1984).

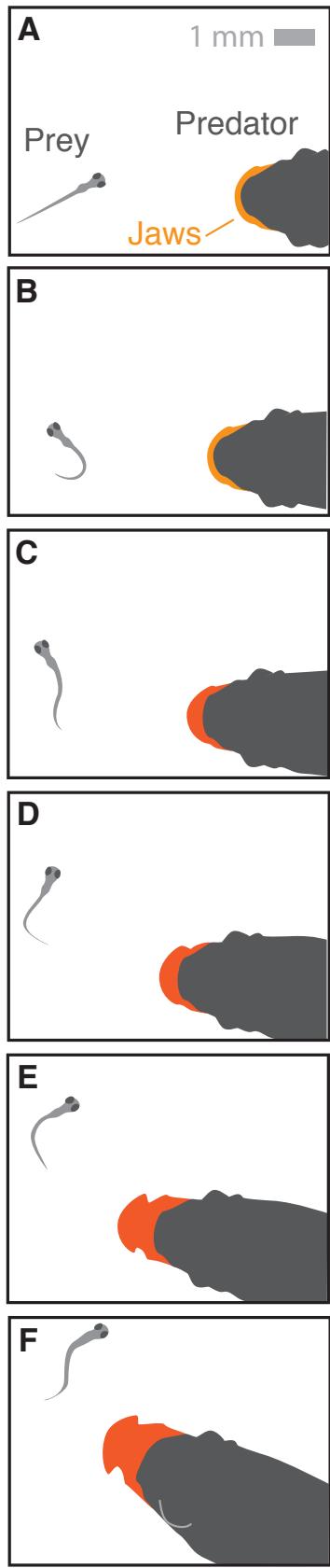
<sup>271</sup> **References**

- <sup>272</sup> **Arnott, S. A., Neil, D. M. and Ansell, A. D.** (1999). Escape trajectories of the brown  
<sup>273</sup> shrimp *Crangon crangon*, and a theoretical consideration of initial escape angles from  
<sup>274</sup> predators. *J. Exp. Biol.* **202**, 193–209.
- <sup>275</sup> **Briggs, J. P.** (2002). The zebrafish: A new model organism for integrative physiology. *Am.  
276 J. Physiol. Regulatory Integrative Comp. Physiol* **282**, R3–R9.
- <sup>277</sup> **Budick, S. A. and O’Malley, D. M.** (2000). Locomotor repertoire of the larval zebrafish:  
<sup>278</sup> Swimming, turning and prey capture. *J. Exp. Biol.* **203**, 2565–2579.
- <sup>279</sup> **Combes, S. A., Rundle, D. E., Iwasaki, J. M. and Crall, J. D.** (2012). Linking biome-  
<sup>280</sup> chanics and ecology through predator–prey interactions: flight performance of dragonflies  
<sup>281</sup> and their prey. *J. Exp. Biol.* **215**, 903–913.
- <sup>282</sup> **Dill, L.** (1974). Escape response of zebra danio (*Brachydanio-Rerio*). 1. Stimulus for Escape.  
<sup>283</sup> *Anim. Behav.* **22**, 711–722.
- <sup>284</sup> **Domenici, P., Batty, R. S., Simila, T. and Ogam, E.** (2000). Killer whales (*Orcus  
285 orca*) feeding on schooling herring (*Clupea harengus*) using underwater tail-slaps:  
<sup>286</sup> kinematic analyses of field observations. *J. Exp. Biol.* **203**, 283–294.
- <sup>287</sup> **Domenici, P. and Blagburn, J. M.** (2011). Animal escapology I: theoretical issues and  
<sup>288</sup> emerging trends in escape trajectories. *J. Exp. Biol.* **214**, 2463–2473.
- <sup>289</sup> **Domenici, P., Booth, D., Blagburn, J. M. and Bacon, J. P.** (2008). Cockroaches  
<sup>290</sup> keep predators guessing by using preferred escape trajectories. *Curr. Biol.* **18**, 1792–1796.

- <sup>291</sup> **Emlen, D. J.** (2014). *Animal Weapons: The Evolution of Battle*. New York: Macmillan.
- <sup>292</sup> **Evans, D. L. and Schmidt, J. O.** (1990). *Insect Defenses: Adaptive Mechanisms and*  
<sup>293</sup> *Strategies of Prey and Predators*. Albany, NY: SUNY Press.
- <sup>294</sup> **Ghose, K., Horiuchi, T. K., Krishnaprasad, P. S. and Moss, C. F.** (2006). Echolo-  
<sup>295</sup> cating Bats Use a Nearly Time-Optimal Strategy to Intercept Prey. *PLoS biology* **4**,  
<sup>296</sup> e108.
- <sup>297</sup> **Heuch, P. A., Doall, M. H. and Yen, J.** (2007). Water flow around a fish mimic attracts  
<sup>298</sup> a parasitic and deters a planktonic copepod. *Journal Of Plankton Research* **29**, i3–i16.
- <sup>300</sup> **Higham, T. E.** (2007). Feeding, fins and braking maneuvers: locomotion during prey  
<sup>301</sup> capture in centrarchid fishes. *J. Exp. Biol.* **210**, 107–117.
- <sup>302</sup> **Higham, T. E., Malas, B., Jayne, B. C. and Lauder, G. V.** (2005). Constraints on  
<sup>303</sup> starting and stopping: behavior compensates for reduced pectoral fin area during braking  
of the bluegill sunfish *Lepomis macrochirus*. *J. Exp. Biol.* **208**, 4735–4746.
- <sup>304</sup> **Howland, H. C.** (1974). Optimal strategies for predator avoidance: The relative importance  
<sup>305</sup> of speed and manoeuvrability. *J. Theor. Biol.* **47**, 333–350.
- <sup>306</sup> **Humphries, D. A. and Driver, P. M.** (1970). Protean defence by prey animals. *Oecologia*  
<sup>307</sup> **5**, 285–302.
- <sup>308</sup> **Isaacs, R.** (1965). *Differential Games: A Mathematical Theory with Applications to Warfare*  
<sup>309</sup> *and Pursuit, Control and Optimization*. New York: John Wiley and Sons, Inc.

- 310 **Kane, E. A. and Higham, T. E.** (2011). The integration of locomotion and prey capture  
311 in divergent cottid fishes: functional disparity despite morphological similarity. *J. Exp.*  
312 *Biol.* **214**, 1092–1099.
- 313 **Kane, E. A. and Higham, T. E.** (2014). Modelled three-dimensional suction accuracy  
314 predicts prey capture success in three species of centrarchid fishes. *J., Roy. Soc. Interface*  
315 **11**, 20140223.
- 316 **Kane, S. A. and Zamani, M.** (2014). Falcons pursue prey using visual motion cues: new  
317 perspectives from animal-borne cameras. *J. Exp. Biol.* **217**, 225–234.
- 318 **Kullberg, C., Jakobsson, S. and Fransson, T.** (1998). Predator-induced take-off strat-  
319 egy in great tits (*Parus major*). *Proceedings of the Royal Society of London. Series B:*  
320 *Biological Sciences* **265**, 1659–1664.
- 321 **McLean, D. L. and Fethcho, J. R.** (2011). Movement, technology and discovery in the  
322 zebrafish. *Curr. Opin. Neurobiol.* **21**, 110–115.
- 323 **Müller, U. K. and van Leeuwen, J. L.** (2004). Swimming of larval zebrafish: ontogeny  
324 of body waves and implications for locomotory development. *J. Exp. Biol.* **207**, 853–868.
- 325 **Ruxton, G. D., Sherratt, T. N. and Speed, M.** (2004). *Avoiding Attack: The Evolu-*  
326 *tionary Ecology of Crypsis, Warning Signals and Mimicry*. Oxford: OUP Oxford.
- 327 **Stewart, W. J., Cardenas, G. S. and McHenry, M. J.** (2013). Zebrafish larvae evade  
328 predators by sensing water flow. *J. Exp. Biol.* **216**, 388–398.

- 329 Stewart, W. J., Nair, A., Jiang, H. and McHenry, M. J. (2014). Prey fish escape by  
330 sensing the bow wave of a predator. *J. Exp. Biol.* **217**, 4328–4336.
- 331 Wainwright, P. C., Ferry-Graham, L., Waltzek, T. B., Carroll, A. M., Hulsey,  
332 C. D. and Grubich, J. R. (2001). Evaluating the use of ram and suction during prey  
333 capture by cichlid fishes. *J. Exp. Biol.* **204**, 3039–3051.
- 334 Webb, J. N. (2007). *Game Theory: Decisions, Interaction and Evolution*. London:  
335 Springer.
- 336 Weihs, D. (1973). The mechanism of rapid starting of slender fish. *Biorheology* **10**, 343–350.
- 337 Weihs, D. and Webb, P. W. (1984). Optimal avoidance and evasion tactics in predator-  
338 prey interactions. *J. Theor. Biol.* **106**, 189–206.
- 339 Wilson, A. M., Lowe, J. C., Roskilly, K., Hudson, P. E., Golabek, K. A. and  
340 McNutt, J. W. (2013). Locomotion dynamics of hunting in wild cheetahs. *Nature* **498**,  
341 185–189.



**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 protraction by the jaws of the predator (orange). (C–D) The predator initiates a strike, which is visible from jaw protraction (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).

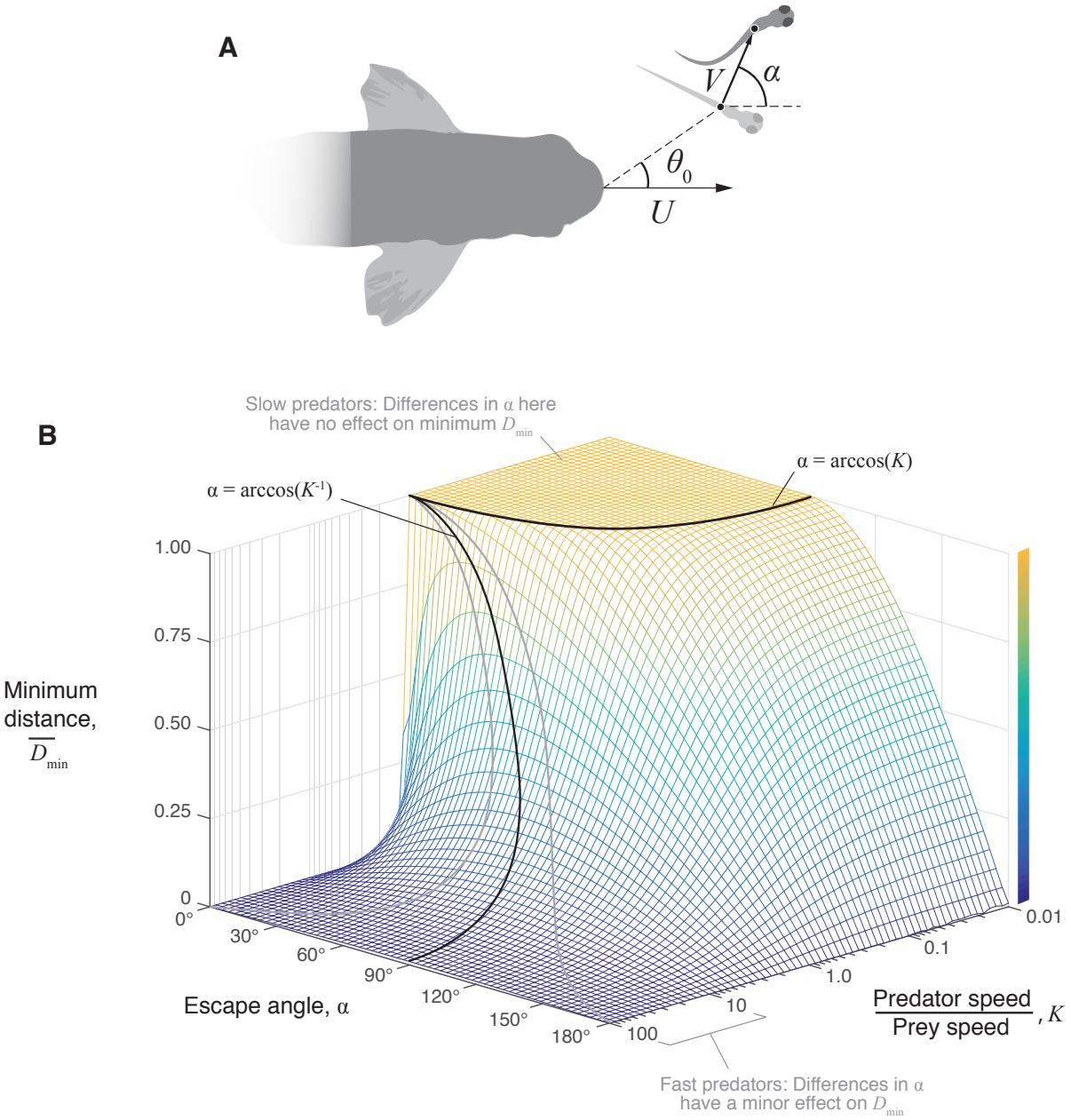
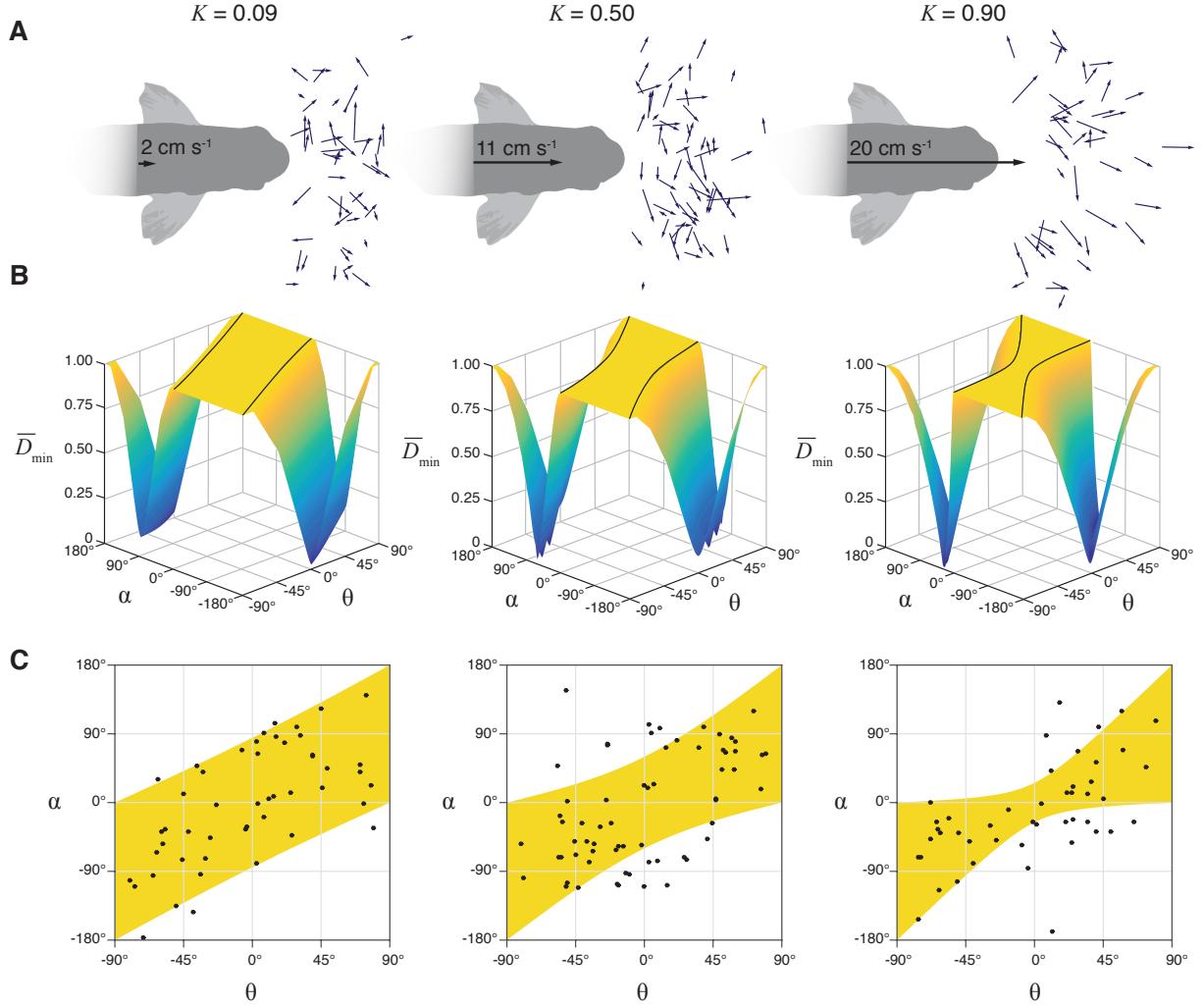


Figure 2: **A pursuit–evasion model for predator–prey interactions in fish.** (A) Pursuit–evasion models consider the motion of a predator (viewed from dorsal perspective) with speed  $U$  and a prey with speed  $V$  and escape angle  $\alpha$ . Some versions of this model consider prey positioned lateral 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<sub>c</sub>1 by Wehs and Webb (1984)). 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  $20 \text{ cm s}^{-1}$ ) (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( $\alpha$ ) and initial position ( $\theta_0$ ). 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**.

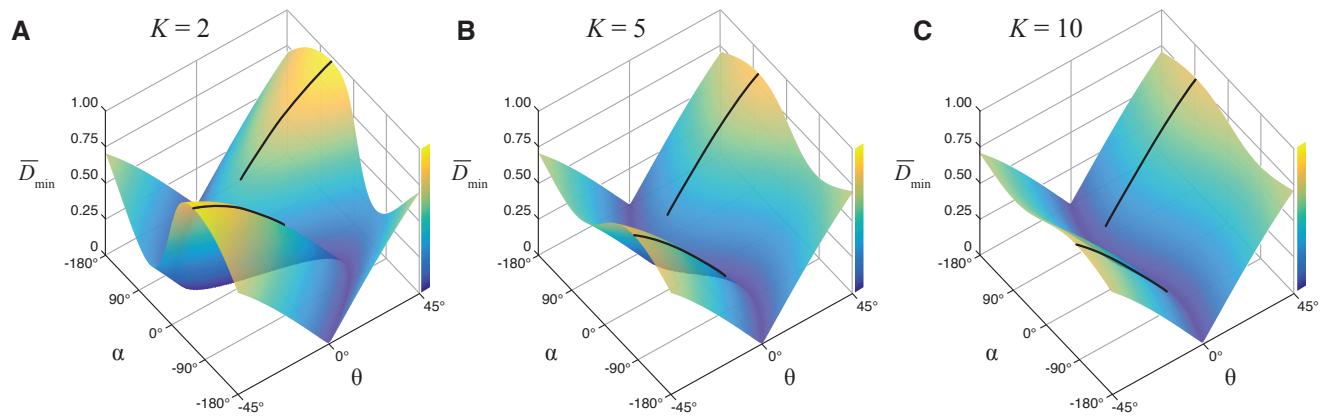


Figure 4: **Evasive performance when the predator is faster than the prey.** Numerical simulations calculated the minimum distance for variable initial position ( $\theta_0$ ) and escape angle ( $\alpha$ ) of the prey for predators that are faster than the prey by a factor of two (A), five (B), and ten (C).