

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

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## Abstract

5 Predator-prey interactions in fish are commonly studied with an interest in deter-  
6 mining whether prey adopt an optimal strategy to evade predators. However, it is  
7 not clear under what circumstances an optimal strategy aids a prey's survival. Here  
8 we examine the theoretical consequences of deviation from optimal strategy for pred-  
9 ators that approach at different speeds. With a focus on the minimum distance between  
10 predator and prey, we simulated these interactions with numerical and analytical math-  
11 ematics and compared our predictions with measurements in zebrafish (*Danio rerio*).  
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, which is the case for  
16 zebrafish. Therefore, the escape angle either has no optimum or has a minor effect on  
17 predator-prey interactions in many situations where the predator is either slower or  
18 much faster than the prey. Optimal strategy is therefore most meaningful when prey  
19 are approached by a predator of intermediate speed. It remains to be seen whether  
20 prey behave optimally in this domain or whether optimal responses serve to enhance  
21 survivorship.

## 22 1 Introduction

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

38 Pursuit models are an area of game theory that offers a basis for examining locomotor  
39 behavior in strategic terms. There is recent interest in revisiting these models (e.g. Howland,  
40 1974; Weihs and Webb, 1984a) with experimental studies that consider the behavior of both  
41 predators and prey. This includes work on running vertebrates (e.g. Wilson et al., 2013),  
42 birds (e.g. Hedenström and Rosén, 2001; Kullberg et al., 1998) and bats (e.g. Ghose et al.,  
43 2006) in flight, running insects (Domenici et al., 2008), flying insects (e.g. Combes et al.,

44 2012), and swimming zooplankton (e.g. Arnott et al., 1999; Heuch et al., 2007) and fishes  
45 (e.g. Domenici et al., 2000). These efforts offer the potential to reveal how sensory and motor  
46 systems govern the outcome of predator–prey interactions.

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

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

67 and the benefit of being unpredictable.

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

## 79 2 Optimal prey strategy

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

88 The payoff is a quantity used in game models to define the beneficial or detrimental  
89 consequences of playing with a particular strategy (Webb, 2007). For pursuit models, the  
90 payoff is often defined as the minimum distance between predator and prey. This quantity  
91 reflects the condition where the predator has the best opportunity to capture the prey. The  
92 optimal strategy for an evasive prey is therefore defined as the escape angle that yields the  
93 greatest minimum distance (Weihs and Webb, 1984).

94 Predicting the distance between predator and prey requires relatively few parameters  
95 under some simplifying assumptions. In the rapid events of a predatory strike, it is reasonable  
96 to approximate the predator's motion as a constant speed,  $U$ . If one neglects the acceleration  
97 period of the fast start, then the prey's motion may be approximated with a constant speed,  
98  $V$ , at an escape angle  $\alpha$ , defined with respect to the heading of the predator (Fig. 1A).  
99 Under these conditions, the distance between predator and prey,  $D$ , may be calculated over  
100 time:

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

101 where  $X_0$  is the starting position of the prey.

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

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

106 where  $K$  indicates the speed of the predator relative to the prey ( $K = U/V$ ). Weihs and  
107 Webb observed that this equation yields negative values of time where  $K < 1$  and is therefore

<sup>108</sup> only useful when the predator is faster than the prey (Weihs and Webb, 1984). The minimum  
<sup>109</sup> distance was consequently determined for  $K > 1$  by solving for distance (Eqn. 1) at  $t_{\min}$ :

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

<sup>110</sup> where  $\overline{D}_{\min}$  is the minimum distance normalized by the starting position of the prey.

<sup>111</sup> Finally, the optimal strategy for the prey may be determined by finding the escape angle  
<sup>112</sup> that yields the greatest minimum distance. This occurs where the derivative of Eqn. 3 with  
<sup>113</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>114</sup> Among the solutions that satisfy this equation, Weihs and Webb proposed that the following  
<sup>115</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>116</sup> We added the  $\pm$  symbol to this expression to indicate that prey are equally effective if  
<sup>117</sup> escaping at an optimal angle toward the left ( $\alpha > 0$ ), or right ( $\alpha < 0$ ) of the predator's  
<sup>118</sup> heading. For relatively fast prey ( $K \leq 1$ ), Weihs and Webb suggested that the optimal  
<sup>119</sup> solution consists of swimming directly away from the predator ( $\alpha = 0$ ) (Weihs and Webb,  
<sup>120</sup> 1984). Therefore, for any predator speed, this model offers predictions for how a prey can  
<sup>121</sup> direct its escape to maximize its chances for survival by creating the greatest distance from  
<sup>122</sup> a predator.

<sup>123</sup> **3 When optimal strategy matters**

<sup>124</sup> An optimum adopts a different meaning if it corresponds to a shallow peak in performance or  
<sup>125</sup> defines a local peak that is much smaller than the global maximum. We considered whether  
<sup>126</sup> these conditions exist in evasion strategy by calculating how the payoff in this pursuit model,  
<sup>127</sup> the minimum distance (Weihs and Webb, 1984a), varies with escape angle and the relative  
<sup>128</sup> speed of the predator. This was considered by formulating a performance landscape of prey  
<sup>129</sup> strategy. As an alternative to analytical mathematics (Eqn. 3), we first formulated this  
<sup>130</sup> landscape with a numerical approach that is simple enough to execute in a spreadsheet,  
<sup>131</sup> but which we implemented in Matlab (MathWorks, Natick, MA, USA). This was done by  
<sup>132</sup> defining a series of time values at an equal interval, which was used to calculate the positions  
<sup>133</sup> 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  
<sup>134</sup> minimum value of the distance between them was determined in this way for variable escape  
<sup>135</sup> angle and predator speed, over a range of  $K$  and  $\alpha$  values (Fig. 2B). This yielded results that  
<sup>136</sup> were coincident with the analytical equation for  $\bar{D}_{\min}$  formulated by Weihs and Webb (1984)  
<sup>137</sup> for relatively fast predators ( $K > 1$ , Eqn. 3). However, the advantage of the numerical  
<sup>138</sup> calculations was that they allowed us to examine variation in the minimum distance for  
<sup>139</sup> slower predators (i.e.  $K < 1$ ) as well. The resulting performance landscape (Fig. 2B)  
<sup>140</sup> illustrates how the minimum distance varies over a broad range of values in the relative  
<sup>141</sup> speed of the predator and escape angle of the prey.

<sup>142</sup> Our results suggest that the fast start is unlikely to be effective at any escape angle  
<sup>143</sup> when a prey is approached by a very fast predator. For example, if a predator is an order  
<sup>144</sup> of magnitude faster than its prey (i.e.  $K = 10$ ), then the prey can do no better than

145 displace its body by 10% of its initial distance from the predator (Fig. 2B). In addition,  
 146 differences in escape angle have little effect on the minimum distance. An escape that is  
 147 24.5° larger or smaller than the optimum yields a minimum distance that is less than the  
 148 value at the optimum by 0.1 (i.e. 1% of the starting position of the prey). These metrics  
 149 become increasingly unfavorable for the prey when approached by an even faster predator  
 150 (Fig. 2B). At these speeds, inaccuracy in the feeding strike is likely a more decisive factor  
 151 to prey survival than anything the prey may do in response.

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

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

159 A prey achieves an optimal escape ( $\bar{D}_{\min} = 1$ ) when the distance function only increases  
 160 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  
 161 proposed as the optimal direction (Weihs and Webb, 1984). However, it also holds true  
 162 that distance increases for another solution to Eqn. 4 ( $\alpha = \pm \arccos K$ ) and all values in  
 163 between. Therefore, the following defines the domain of optimal directions when the prey is  
 164 faster than the predator ( $K < 1$ ):

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

<sub>165</sub> This analysis suggests that if the escape response of a prey is capable of exceeding the  
<sub>166</sub> approach speed of the predator, then a wide range of angles yield equally successful escapes  
<sub>167</sub> for the prey and thereby define a performance plateau.

<sub>168</sub> The domain where optimal the optimal strategy matters the most resides between where  
<sub>169</sub> the prey and predator are equivalent in speed and where the predator is an order of magnitude  
<sub>170</sub> faster ( $1 < K < 10$ ). In this domain, prey are capable of attaining appreciable minimum  
<sub>171</sub> distance values and there is a penalty for deviating from the optimal angle (Fig. 2B).  
<sub>172</sub> Therefore, a prey fish has a strong incentive to conform to the optimal prediction when  
<sub>173</sub> encountering a slightly faster predator.

## <sub>174</sub> 4 Comparing models with measurements

<sub>175</sub> We were interested in examining whether optimal strategy matters under experimental con-  
<sub>176</sub> ditions. This was addressed with recent measurements on larval zebrafish, which are preyed  
<sub>177</sub> upon by adults of the same species (Stewart et al., 2013). This work included experiments  
<sub>178</sub> that used a robot to simulate the approach of a predator toward prey in the dark, with  
<sub>179</sub> recordings of the position at which the prey responded with a fast start and the direction of  
<sub>180</sub> that response (Stewart et al., 2014). This evasive action was stimulated by the lateral line  
<sub>181</sub> system of the prey, which detected the water flow generated by the approaching predator.

<sub>182</sub> As detailed above, the predictions of the model depend on the speed of the predator  
<sub>183</sub> relative to the prey. The approach speed of the robot, and consequently  $K$ , was varied to  
<sub>184</sub> span the range of values observed for a live predator (Stewart et al., 2013). Our calculations  
<sub>185</sub> of  $K$  used a prey speed ( $U = 22 \text{ cm s}^{-1}$ ) from the literature that approximates the maximum

186 value attained during a fast start for larvae of this species (Budick and O’Malley, 2000; Müller  
 187 and van Leeuwen, 2004). As a consequence of the relatively slow approach made by these  
 188 suction-feeding predators, the prey had the potential to move faster at all approach speeds,  
 189 which yielded  $K$ -values that were uniformly less than unity (Fig. 3A).

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

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

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

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

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

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

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

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

$$\bar{D}_{\min} = 1 \text{ if } 0 \leq \alpha \leq [|\theta_0| + \arccos(K \cos |\theta_0|)], \quad (11)$$

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

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

225 **5 Predator strategy**

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

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

244 We conducted a series of simulations that examine the effect of an inaccurate strike by  
245 a fast predator. As in our comparison with experimental results (Fig. 3), we calculated  
246 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 measured of inaccuracy neglects the increasing challenge of correct timing in the opening of the jaws at increasing approach speeds, 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, the minimum distance varies substantially with both escape direction and strike accuracy (Fig. 4A). For example, the optimal escape angle ( $\alpha_{\text{opt}} = 60.0^\circ$ ) generates a minimum distance ( $\bar{D}_{\min} = 0.71$ ) that is more than two-orders of magnitude better than what may be achieved with the least effective escape direction ( $\bar{D}_{\min} = 0.002$ ) when the prey is positioned  $15^\circ$  from the predator's heading. This advantage in minumum distance is not greatly reduced ( $\bar{D}_{\min} = 0.50$  at  $\alpha_{\text{opt}} = 60^\circ$ ) if the predator successfully aligns its strike ( $\theta_0 = 0^\circ$ ). However, the escape angle plays a reduced role in aiding predator evasion at faster approach speeds. For example, when the predator is 10-times faster (Fig. 4C) and inaccurate ( $\theta_0 = 15^\circ$ ), then the optimal escape angle ( $\alpha_{\text{opt}} = 84.3^\circ$ ) is only slightly more than twice the value ( $\bar{D}_{\min} = 0.35$ ) for the least effective angle ( $\bar{D}_{\min} = 0.16$ ). Furthermore, the optimal minimum distance is ( $\bar{D}_{\min} = 0.10$ ) is 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.

<sub>268</sub> **6 Conclusions**

<sub>269</sub> The present results offer a new perspective on predator-prey strategy.

<sub>270</sub> The model's assumptions could be violated by the system. For example, a prey fish

<sub>271</sub> cannot move in an optimal direction that maximizes its distance from a predator if it cannot

<sub>272</sub> detect the predator's speed (Weihs and Webb, 1984a).

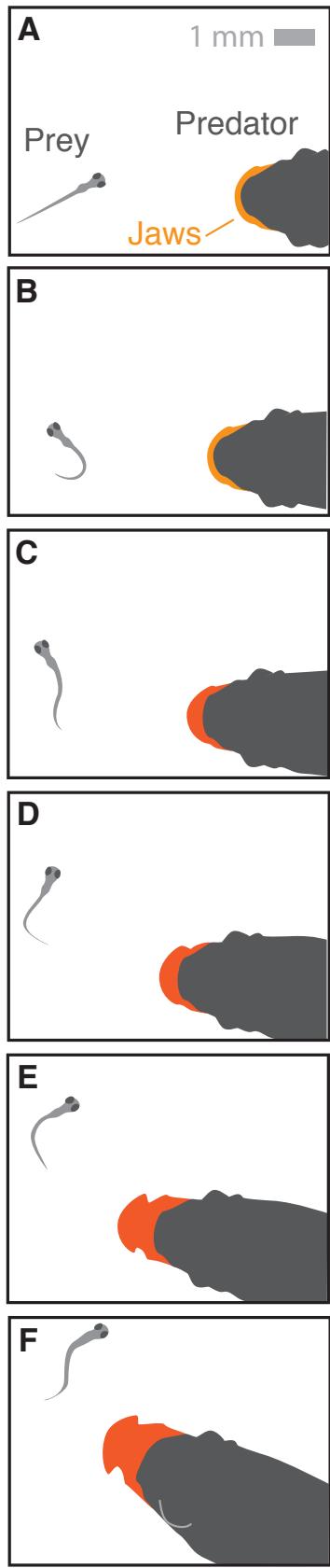
<sup>273</sup> **References**

- <sup>274</sup> **Arnott, S. A., Neil, D. M. and Ansell, A. D.** (1999). Escape trajectories of the brown  
<sup>275</sup> shrimp *Crangon crangon*, and a theoretical consideration of initial escape angles from  
<sup>276</sup> predators. *J. Exp. Biol.* **202**, 193–209.
- <sup>277</sup> **Briggs, J. P.** (2002). The zebrafish: A new model organism for integrative physiology. *Am.  
278 J. Physiol. Regulatory Integrative Comp. Physiol* **282**, R3–R9.
- <sup>279</sup> **Budick, S. A. and O’Malley, D. M.** (2000). Locomotor repertoire of the larval zebrafish:  
<sup>280</sup> Swimming, turning and prey capture. *J. Exp. Biol.* **203**, 2565–2579.
- <sup>281</sup> **Combes, S. A., Rundle, D. E., Iwasaki, J. M. and Crall, J. D.** (2012). Linking biome-  
<sup>282</sup> chanics and ecology through predator–prey interactions: flight performance of dragonflies  
<sup>283</sup> and their prey. *J. Exp. Biol.* **215**, 903–913.
- <sup>284</sup> **Dill, L.** (1974). Escape response of zebra danio (*Brachydanio-Rerio*). 1. Stimulus for Escape.  
<sup>285</sup> *Anim. Behav.* **22**, 711–722.
- <sup>286</sup> **Domenici, P., Batty, R. S., Simila, T. and Ogam, E.** (2000). Killer whales (*Orcus  
287 cinus orca*) feeding on schooling herring (*Clupea harengus*) using underwater tail-slaps:  
<sup>288</sup> kinematic analyses of field observations. *J. Exp. Biol.* **203**, 283–294.
- <sup>289</sup> **Domenici, P. and Blagburn, J. M.** (2011). Animal escapology I: theoretical issues and  
<sup>290</sup> emerging trends in escape trajectories. *J. Exp. Biol.* **214**, 2463–2473.
- <sup>291</sup> **Domenici, P., Booth, D., Blagburn, J. M. and Bacon, J. P.** (2008). Cockroaches  
<sup>292</sup> keep predators guessing by using preferred escape trajectories. *Curr. Biol.* **18**, 1792–1796.

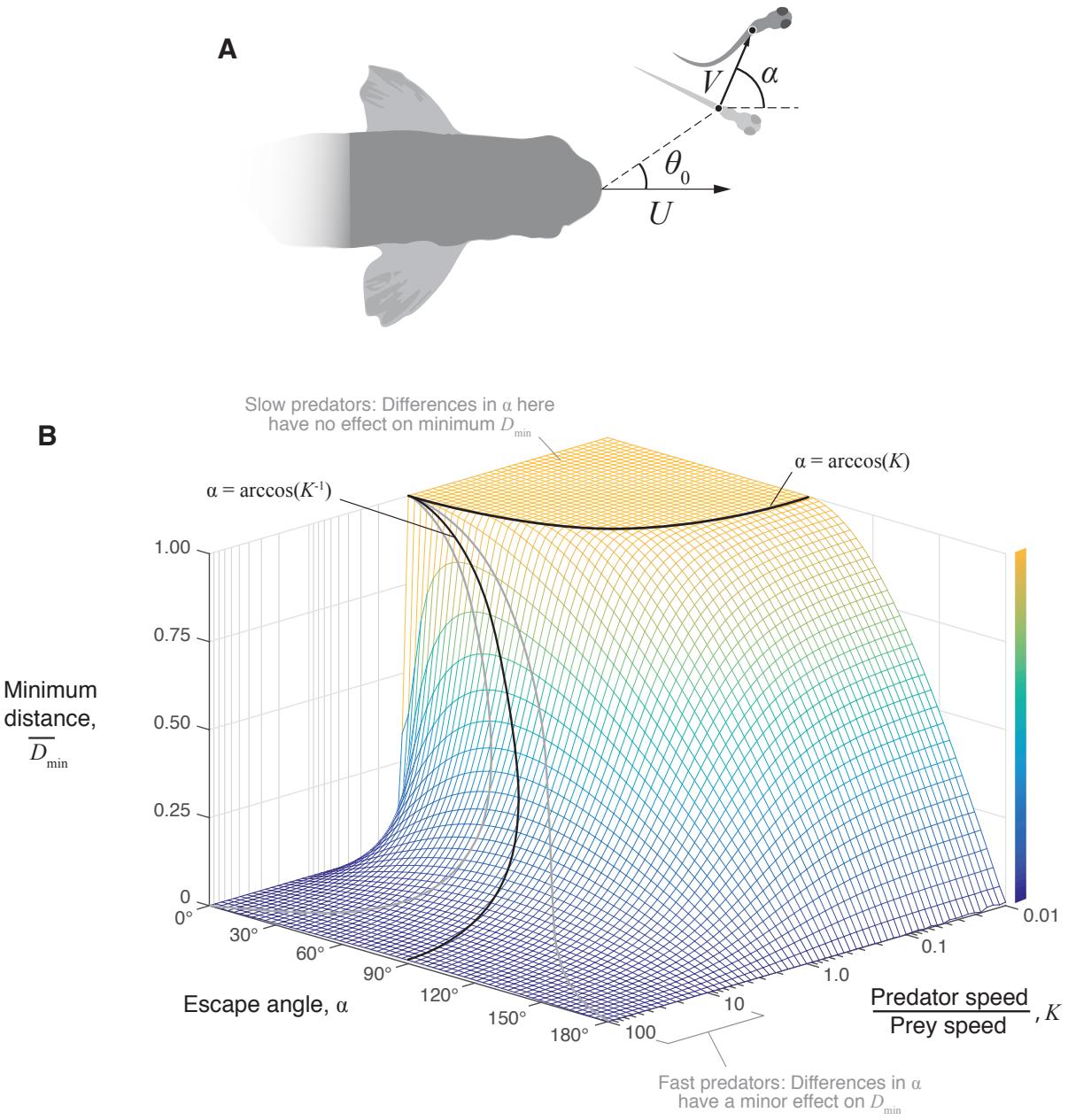
- <sup>293</sup> **Emlen, D. J.** (2014). *Animal Weapons: The Evolution of Battle*. New York: Macmillan.
- <sup>294</sup> **Evans, D. L. and Schmidt, J. O.** (1990). *Insect Defenses: Adaptive Mechanisms and*
- <sup>295</sup> *Strategies of Prey and Predators*. Albany, NY: SUNY Press.
- <sup>296</sup> **Ghose, K., Horiuchi, T. K., Krishnaprasad, P. S. and Moss, C. F.** (2006). Echolo-
- <sup>297</sup> cating Bats Use a Nearly Time-Optimal Strategy to Intercept Prey. *PLoS biology* **4**,
- <sup>298</sup> e108.
- <sup>299</sup> **Hedenström, A. and Rosén, M.** (2001). Predator versus prey: on aerial hunting and
- <sup>300</sup> escape strategies in birds. *Behavioral Ecology* **12**, 150–156.
- <sup>301</sup> **Heuch, P. A., Doall, M. H. and Yen, J.** (2007). Water flow around a fish mimic attracts
- <sup>302</sup> a parasitic and deters a planktonic copepod. *Journal Of Plankton Research* **29**, i3–i16.
- <sup>303</sup> **Higham, T. E.** (2007). Feeding, fins and braking maneuvers: locomotion during prey
- <sup>304</sup> capture in centrarchid fishes. *J. Exp. Biol.* **210**, 107–117.
- <sup>305</sup> **Higham, T. E., Malas, B., Jayne, B. C. and Lauder, G. V.** (2005). Constraints on
- <sup>306</sup> starting and stopping: behavior compensates for reduced pectoral fin area during braking
- <sup>307</sup> of the bluegill sunfish *Lepomis macrochirus*. *J. Exp. Biol.* **208**, 4735–4746.
- <sup>308</sup> **Howland, H. C.** (1974). Optimal strategies for predator avoidance: The relative importance
- <sup>309</sup> of speed and manoeuvrability. *J. Theor. Biol.* **47**, 333–350.
- <sup>310</sup> **Humphries, D. A. and Driver, P. M.** (1970). Protean defence by prey animals. *Oecologia*
- <sup>311</sup> **5**, 285–302.

- 312 **Isaacs, R.** (1965). *Differential Games: A Mathematical Theory with Applications to Warfare*  
313      and Pursuit, Control and Optimization. New York: John Wiley and Sons, Inc.
- 314 **Kane, S. A. and Zamani, M.** (2014). Falcons pursue prey using visual motion cues: new  
315      perspectives from animal-borne cameras. *J. Exp. Biol.* **217**, 225–234.
- 316 **Kullberg, C., Jakobsson, S. and Fransson, T.** (1998). Predator-induced take-off strat-  
317      egy in great tits (*Parus major*). *Proceedings of the Royal Society of London. Series B:*  
318      *Biological Sciences* **265**, 1659–1664.
- 319 **McLean, D. L. and Fethcho, J. R.** (2011). Movement, technology and discovery in the  
320      zebrafish. *Curr. Opin. Neurobiol.* **21**, 110–115.
- 321 **Müller, U. K. and van Leeuwen, J. L.** (2004). Swimming of larval zebrafish: ontogeny  
322      of body waves and implications for locomotory development. *J. Exp. Biol.* **207**, 853–868.
- 323 **Ruxton, G. D., Sherratt, T. N. and Speed, M.** (2004). *Avoiding Attack: The Evolu-*  
324      *tionary Ecology of Crypsis, Warning Signals and Mimicry*. Oxford: OUP Oxford.
- 325 **Stewart, W. J., Cardenas, G. S. and McHenry, M. J.** (2013). Zebrafish larvae evade  
326      predators by sensing water flow. *J. Exp. Biol.* **216**, 388–398.
- 327 **Stewart, W. J., Nair, A., Jiang, H. and McHenry, M. J.** (2014). Prey fish escape by  
328      sensing the bow wave of a predator. *J. Exp. Biol.* **217**, 4328–4336.
- 329 **Wainwright, P. C., Ferry-Graham, L., Waltzek, T. B., Carroll, A. M., Hulsey,**  
330      **C. D. and Grubich, J. R.** (2001). Evaluating the use of ram and suction during prey  
331      capture by cichlid fishes. *J. Exp. Biol.* **204**, 3039–3051.

- <sup>332</sup> **Webb, J. N.** (2007). *Game Theory: Decisions, Interaction and Evolution*. London:
- <sup>333</sup> Springer.
- <sup>334</sup> **Weihs, D.** (1973). The mechanism of rapid starting of slender fish. *Biorheology* **10**, 343–350.
- <sup>335</sup> **Weihs, D. and Webb, P. W.** (1984a). Optimal avoidance and evasion tactics in predator-
- <sup>336</sup> prey interactions. *J. Theor. Biol.* **106**, 189–206.
- <sup>337</sup> **Weihs, D. and Webb, P. W.** (1984b). Optimal avoidance and evasion tactics in predator-
- <sup>338</sup> prey interactions. *Journal of Theoretical Biology* **106**, 189–206.
- <sup>339</sup> **Wilson, A. M., Lowe, J. C., Roskilly, K., Hudson, P. E., Golabek, K. A. and**
- <sup>340</sup> **McNutt, J. W.** (2013). Locomotion dynamics of hunting in wild cheetahs. *Nature* **498**,
- <sup>341</sup> 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 model for predator-prey interactions in fish.** (A) Pursuit 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 to examine variation in the minimum distance. At  $K > 1$ , the optimal angle (black curve) was predicted analytically (Eqn. refK<sub>i</sub>1 by Weihs and Webb (1984b)). Deviation from the optimum by  $0.1\bar{D}_{\min}$  (gray curves) is shown to increase at greater values of  $K$ . The performance plateau where  $D_{\min} = 1$  is predicted by Eqn. 7.

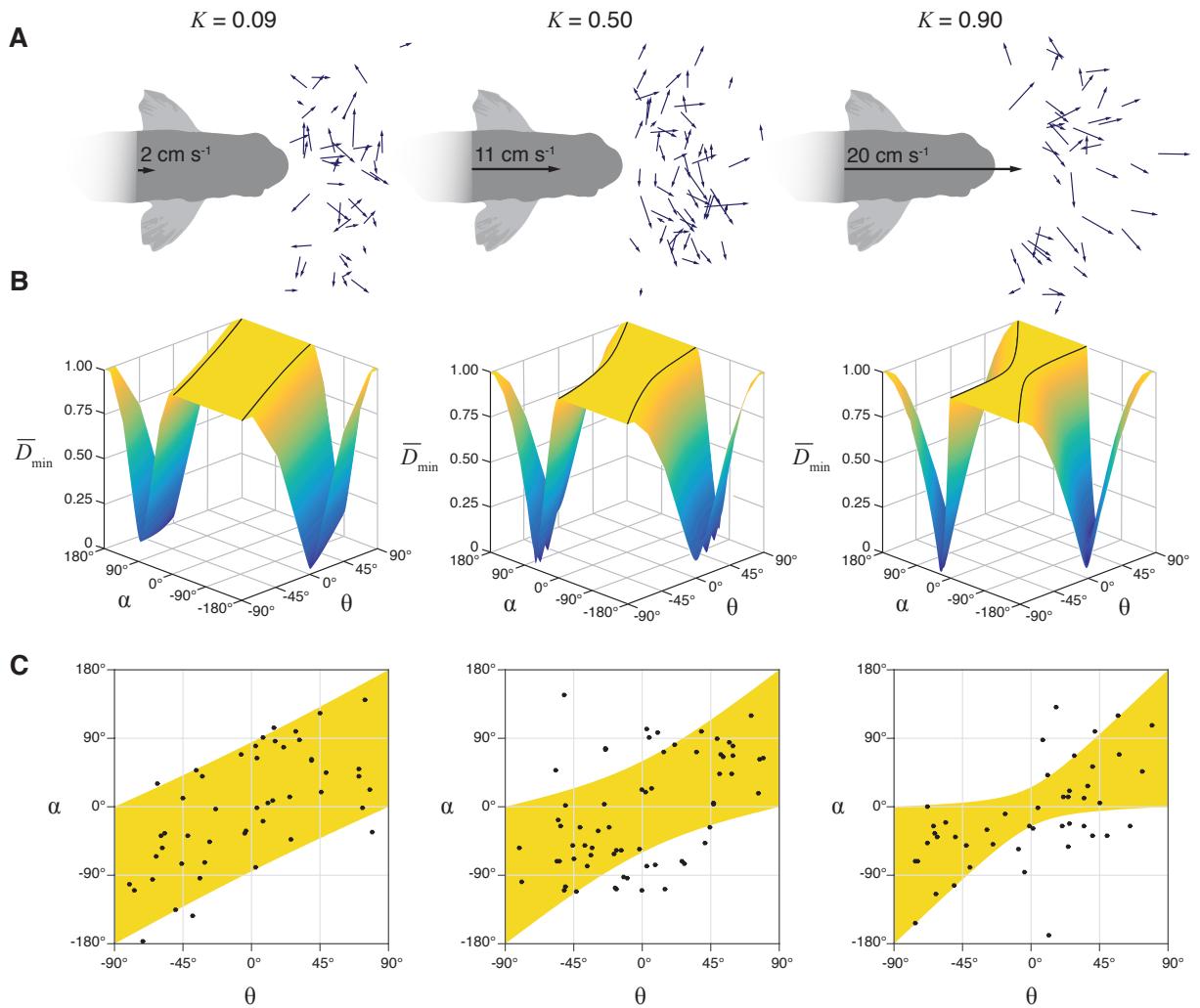


Figure 3: Model predictions and measurements of the fast start. (A)

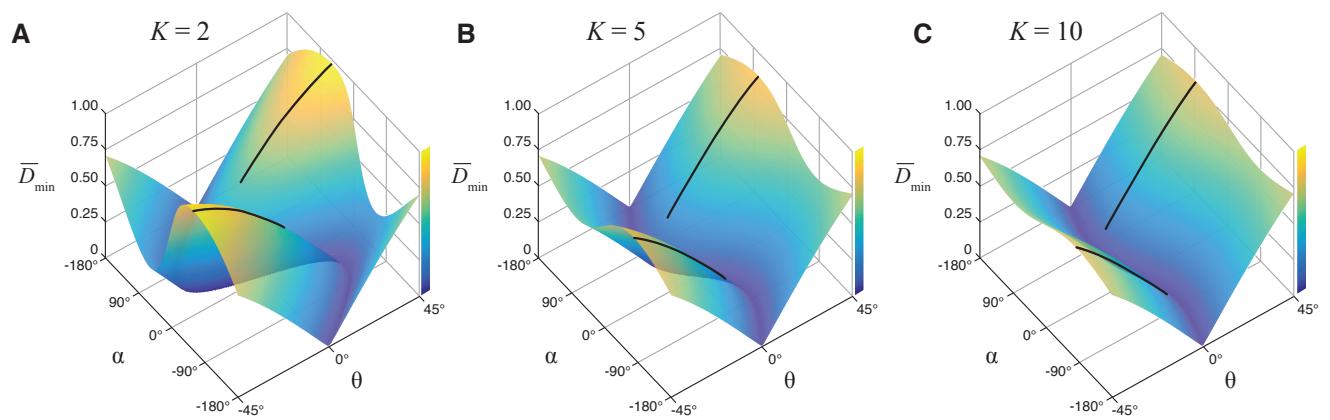


Figure 4: Title. (A)