

1 **Effect of initial body orientation on escape probability in prey fish escaping from**
2 **predators**

3

4 Running title: Effect of orientation on escape

5

6 Names and affiliations of authors:

7 Hibiki Kimura, Yuuki Kawabata*

8 Graduate School of Fisheries and Environmental Sciences, Nagasaki University,

9 Bunkyo-machi, Nagasaki 852-8521, Japan

10

11 *Corresponding author: yuuki-k@nagasaki-u.ac.jp

12

13 Key words:

14 Attack angle, C-start, Escape response, Fast-start, Kinematics, Predator-prey interaction

15

16 Summary statement:

17 Our predator-prey experiments reveal that the prey's initial body orientation relative to a

18 predator affects the prey's turn angle and its duration, and consequently affects escape

19 probability.

20

21 **Abstract**

22 Since the escape response is crucial to survival and hence to the fitness of species,
23 several studies have attempted to elucidate the kinematic and behavioral components of
24 the response that affect evasion outcome. The prey's body orientation relative to a
25 predator at the onset of the escape response (initial orientation) could affect evasion
26 outcome, because the turn angle and its duration before the initiation of escape
27 locomotion would be smaller when the initial orientation is more away from the
28 predator. We tested this hypothesis by recording the escape responses of juvenile red
29 sea bream (*Pagrus major*) in response to the predatory scorpion fish (*Sebastiscus*
30 *marmoratus*) using a high-speed video camera. Our results show that an increased initial
31 orientation (i.e., more away from the predator) increases escape probability. Our results
32 also indicate that an increase in the initial orientation decreases the turn angle and its
33 duration. The flight initiation distance tends to be small when the initial orientation is
34 away from the predator, suggesting that the prey might have a blind zone of sensory
35 perception. These findings highlight the importance of incorporating initial orientation
36 into both empirical and theoretical studies of the kinematics of predator-prey
37 interactions.

38

39 **Introduction**

40 When exposed to sudden predation threats, most animals exhibit escape responses that
41 include turning swiftly and accelerating forward (Bulbert et al., 2015; Camhi et al.,
42 1978; Webb, 1986). Since the escape response is crucial to survival and hence to the
43 fitness of the species, numerous studies have been conducted to elucidate the
44 environmental and internal factors that affect the behavioral and kinematic components
45 of the escape response (e.g., flight initiation distance, escape trajectory, turning speed,
46 acceleration, etc.) (Bateman and Fleming, 2014; Cooper, 2006; Cooper et al., 2007;
47 Domenici, 2010; Meager et al., 2006). Most of these studies, however, have used
48 artificial stimuli to elicit the escape response, and thus knowledge of the importance of
49 different components of the response in the context of avoiding real predators is still
50 limited.

51 Previous theoretical studies have shown that the outcome of the escape
52 response is dependent on the flight initiation distance, predator and prey speeds, and the
53 escape trajectory (Arnott et al., 1999; Broom and Ruxton, 2005; Domenici, 2002; Weihs
54 and Webb, 1984). Interestingly, however, these studies have not incorporated the prey's
55 initial body orientation with respect to the predator (hereafter, initial orientation) and the
56 prey's turning speed, despite the fact that turning requires additional time prior to the
57 initiation of escape locomotion (King and Comer, 1996), and that initial orientation
58 affects the turn angle (Cooper and Sherbrooke, 2016; Eaton and Emberley, 1991;
59 Kawabata et al., 2016). Empirical studies show that turning speed, as well as the above
60 variables, affects predator evasion (Dangles et al., 2006; Scharf et al., 2003; Stewart et
61 al., 2013; Walker et al., 2005); however, as far as we aware, except for one study
62 (Stewart et al., 2013), no research has been conducted on the effect of initial orientation

63 on escape probability.

64 The C-start escape response of fish and amphibian larvae is one of the most
65 well-studied escape responses in animals (Domenici and Blake, 1997; Eaton et al.,
66 2001). The C-start escape response is composed of three distinct stages based on
67 kinematics: the initial bend (stage 1), the return tail flip (stage 2), and then continuous
68 swimming or coasting (stage 3) (Domenici and Blake, 1997; Weihs, 1973). It has been
69 shown that flight initiation distance, escape speed, turning speed, and escape trajectory
70 affect evasion outcome (Scharf et al., 2003; Stewart et al., 2013; Walker et al., 2005),
71 but the effect of initial orientation remains to be elucidated. The objectives of our study
72 were to determine whether initial orientation affects evasion outcome, and if so, to
73 investigate the mechanisms involved. To achieve these objectives, we recorded the
74 escape responses of juvenile red sea bream [*Pagrus major* (Temminck & Schlegel,
75 1843)] in response to the predatory scorpion fish [*Sebastiscus marmoratus* (Cuvier,
76 1829)] using a high-speed video camera. Since the fish could have spatial bias in
77 detecting the attacking predator (e.g., a sensory blind zone), the effect of initial
78 orientation on the response parameters was also examined. The specific questions
79 addressed were as follows: (1) does an increase in the initial orientation of prey fish
80 (more opposite from the direction of the predator) increase escape probability?; (2) does
81 an increase in the initial orientation decrease the turn angle and its duration?; and (3)
82 does the initial orientation affect responsiveness and flight initiation distance?

83

84 **Results**

85 In general, the predator [*S. marmoratus*, 149.9±17.0 (mean±s.d.) mm total length (TL),
86 *n*=7] approached the prey (*P. major*, 56.1±9.6 mm TL, *n*=46) and then attacked it by

87 opening its mouth. The kinematic stages in which the prey were captured are
88 summarized in Fig. 1. The most prey individuals (43/46: 93%) showed escape responses
89 (C-start), but three (3/46: 7%) did not show responses and were captured by predators.
90 Of the 43 prey that showed escape responses, 19 (19/43: 44%) were captured by
91 predators during stage 1. Of the 24 prey that survived until the end of the stage 1, four
92 (4/24: 17%) were captured by the end of stage 2. No fish were captured during stage 3.
93 Of the total number of prey captured (26), 22 (22/26: 85%) were captured by the end of
94 stage 1. These results indicate that stage 1 is the most critical period for *P. major* to
95 escape from the attack of *S. marmoratus*.

96 The frequency distribution of the initial orientation and the initial
97 orientation–escape probability relationship are shown in Fig. 2. The frequency of initial
98 orientation at 120-180° was lower than at 0-120° (Fig. 2A). Escape probability was
99 highest in the 120-150° initial orientation bin, although 95% confidence intervals based
100 on binomial distributions suggest that there were no significant differences among the
101 different initial orientation bins (Fig. 2B).

102 Differences in the parameters (initial orientation, flight initiation distance, and
103 predator speed) between the successful (escaped) and unsuccessful (captured) escapes
104 are shown in Table 1. The initial orientation of the successful escapes (79.7±43.5°) was
105 larger than that of the unsuccessful ones (64.2±51.0°), and the larger initial orientation
106 significantly increased escape probability (Fig. 3; LR-test, $\chi^2=5.30$, d.f.=1, $P<0.05$). The
107 odds ratio indicates that a 48.0° (1 s.d.) increase in initial orientation increased the
108 escape probability 2.52 times. Increases in flight initiation distance also significantly
109 increased escape probability (Fig. 3; LR test, $\chi^2=17.98$, d.f.=1, $P<0.01$), but the effect of
110 predator speed was insignificant (LR test, $\chi^2=0.23$, d.f.=1, $P=0.63$). The odds ratio of

111 flight initiation distance indicates that an increase of 31.6 mm (1 s.d.) increased the
112 escape probability 6.47 times.

113 There were negative relationships between initial orientation and turn angle
114 (Fig. 4A; $R=-0.61$, $n=24$, $P<0.01$), and between the initial orientation and turn duration
115 (Fig. 4B; $R=-0.41$, $n=24$, $P<0.05$); the effect of the initial orientation on turn angle and
116 turn duration was significant (turn angle: LMM, $F_{1,18.5}=22.88$, $P<0.01$; turn duration:
117 LMM, $F_{1,16.9}=29.56$, $P<0.01$). Additionally, there was a significant positive relationship
118 between the turn angle and its duration ($R=0.53$, $n=24$, $P<0.01$). These results indicate
119 that the turn angle and its duration were larger when the initial orientation was more
120 toward the predator, and smaller when the initial orientation was more away from the
121 predator.

122 There was no observable pattern in the initial orientations of the three prey
123 individuals that did not show escape responses (19.9, 33.4, and 165.7°). The flight
124 initiation distance tended to be shorter when the initial orientation was away from
125 predators (about 150-180°; Fig. 5), although this tendency (the effect of initial
126 orientation on flight initiation distance) was not statistically significant (GAMM,
127 $F=2.10$, estimated d.f.=2.35, estimated residual d.f.=40.92, $P=0.09$). Predator speed
128 significantly increased the flight initiation distance of the prey (GAMM, $F=4.82$,
129 estimated d.f.=1.73, estimated residual d.f.=40.92, $P<0.05$).

130

131 **Discussion**

132 Our results clearly show that an increase in the initial orientation (i.e., more fully away
133 from the predator) increases the probability that *P. major* juveniles will escape from the
134 predatory strikes of *S. marmoratus* (Fig. 3). This result is inconsistent with a study of

135 zebrafish larvae evading adult zebrafish (Stewart et al., 2013), in which escape
136 probabilities were not significantly different among six different initial orientation bins.
137 This discrepancy could be attributed to the different statistical methods used in the two
138 studies, or to species-specific/ontogenetic differences. In the study of the zebrafish
139 larvae, the initial orientation values were categorized into six bins and escape
140 probability was compared among the different bins by calculating 95% confidence
141 intervals. In that analysis, the effects of other variables (i.e., flight initiation distance and
142 predator speed) were not offset. By contrast, our study used a generalized linear mixed
143 model (GLMM) with no binning of the initial orientation values, and it included the
144 other possible variables in the model to offset their variation. In fact, when we analyzed
145 the effect of initial orientation in the same manner as in the study of the zebrafish larvae,
146 the effect of initial orientation on escape probability became statistically insignificant
147 (Fig. 2B). In light of these facts, the binning procedures and/or the large variation in the
148 other variables may have masked the actual effect of initial orientation, and thus initial
149 orientation could actually be a crucial parameter for predator evasion in other fishes as
150 well.

151 Our results also show that an increase in the initial orientation decreases the
152 turn angle and its duration (Fig. 4). This initial orientation–turn angle relationship is
153 consistent with studies of many animal taxa (e.g., other fish, frogs, cockroaches, and
154 lizards) (Camhi and Tom, 1978; Cooper and Sherbrooke, 2016; Eaton and Emberley,
155 1991; King and Comer, 1996). Although a limited number of studies have examined the
156 relationship between turn angle and its duration or between initial orientation and turn
157 duration, it is natural to assume that a larger turn angle requires a longer duration, as has
158 been shown in this study and in a study on frogs (King and Comer, 1996). C-starts and

159 other escape responses start from initial turns, followed by escape locomotion; during
160 the initial turns, the animals do not move large distances but stay close to their initial
161 positions (Camhi et al., 1978; Domenici and Blake, 1997; King and Comer, 1996;
162 Tauber and Camhi, 1995). Therefore, predators would be able to approach prey animals
163 during these initial turns. It is thus likely that initial orientation-mediated turn angle
164 changes affect escape probability by changing the time available for the predator to
165 approach the prey before the initiation of escape locomotion.

166 The flight initiation distance tended to be smaller when the predator
167 approached the prey from behind (Fig. 5). This might be related to a sensory blind zone
168 in the prey. The C-start escape response is triggered by either visual (Dill, 1974),
169 mechanical (Umeda et al., 2016), or sound stimuli (Domenici and Batty, 1997). When it
170 is triggered by visual stimuli there would be a blind zone for the prey (Domenici, 2002;
171 Tyrrell and Fernandez-Juricic, 2015). On the other hand, the lateral line
172 (mechanosensory system) is distributed throughout the body (Dijkgraaf, 1963;
173 Kasumyan, 2003), which may allow 360° perception without any spatial bias. It is also
174 unlikely that there is a spatial bias in detecting sound stimuli. It is thus possible that the
175 *P. major* juveniles relied mainly on visual senses to perform escape responses, and thus
176 the flight initiation distance tended to be smaller when the initial orientation was away
177 from the predator. Further research is clearly needed to clarify the relationship between
178 initial orientation and flight initiation distance, as well as the underlying sensory
179 mechanisms.

180 Considering the time for turning and the sensory blind zone, the optimal initial
181 orientation for prey to escape from predators might be near the edge of the maximum
182 perception range, since this would require a relatively shorter time for turning before

183 escape locomotion, and would allow the prey to respond to the predator's strike from a
184 great enough distance. This hypothesis is consistent with the initial orientation–escape
185 probability relationship, in which the maximum escape probability occurred around
186 120-150° (Fig. 2B). However, the frequency of the initial orientation was not highest
187 around this range: the frequency at 120-180° was smaller than that at 0-120° (Fig. 2A).
188 Because we used naïve hatchery-reared fish that had not experienced any predators, the
189 prey might not have recognized the predator as dangerous, and thus the prey did not
190 adjust the initial orientation in advance. It has been shown that black goby change their
191 posture when a weak stimulus is presented before the strong stimulation that finally
192 elicits an escape response (Turesson et al., 2009). Therefore, prey animals that
193 recognize a predator in advance may adjust their initial orientation to maximize their
194 escape probability, although we should note that predators may also adjust the attack
195 angle (i.e., initial orientation) to maximize predation probability (Webb and Skadsen,
196 1980).

197 Different geometrical models have been proposed to explain the factors
198 affecting escape probability and/or the escape trajectory (Arnott et al., 1999; Corcoran
199 and Conner, 2016; Domenici, 2002; Howland, 1974; Weihs and Webb, 1984), but none
200 of these models have incorporated initial orientation. Furthermore, initial orientation has
201 not been considered in many empirical studies of predator-prey interactions (e.g.,
202 Dangles et al., 2006; Fuiman, 1993; Scharf et al., 2003; Walker et al., 2005). Our results
203 clearly show that initial orientation affects escape probability, and that it can affect
204 flight initiation distance. These findings highlight the importance of incorporating data
205 on initial orientation into both theoretical and empirical studies of predator-prey
206 interactions.

207

208 **Materials and Methods**

209 **Ethics statement**

210 Animal care and experimental procedures were approved by the Animal Care and Use
211 Committee of the Institute for East China Sea Research, Nagasaki University (Permit no.
212 ECSE15-12), in accordance with the Regulations of the Animal Care and Use
213 Committee of Nagasaki University.

214

215 **Fish samples**

216 Hatchery-reared *P. major* ($n=151$) were utilized as prey fish in this study. All individual
217 *P. major* were provided from commercial hatcheries, and were kept in three 200 L
218 polycarbonate tanks at the Institute for East China Sea Research, Nagasaki University,
219 Japan. They were fed with commercial pellets (Otohime C2, Marubeni Nisshin Feed
220 Co., Ltd., Tokyo, Japan) twice a day.

221 As predators, we used *S. marmoratus* ($n=7$), which is a common reef predator
222 around the coast of Japan. *S. marmoratus* usually employs a “stalk-and-attack” tactic.
223 All *S. marmoratus* were collected by hook-and-line around Nagasaki prefecture, Japan.
224 The collected *S. marmoratus* were kept in a glass aquarium (1200×450×450 mm) before
225 the start of the experiment. They were standardly fed krill once every 2-4 days.

226 The position of the center of mass (CM) for *P. major* was estimated by hanging
227 dead fish (54.3 ± 3.3 mm TL, $n=10$) from two different points using a suture and needle
228 (Lefrancois et al., 2005). The CM position from the tip of the head was estimated as
229 0.34 ± 0.01 TL.

230

231 **Experimental procedure**

232 Experiments were performed in a glass aquarium (900×600×300 mm) with seawater to
233 a depth of 100 mm. The water temperature during the experiments was 23.1±0.9°C.
234 White plastic plates with grid lines were placed on the bottom and three sides of the
235 tank; one side (900×300 mm) of the tank was left transparent to record the side view of
236 the fish. A preliminary experiment showed that *S. marmoratus* actively fed in low light
237 conditions, so two LED bulbs covered with red cellophane were used to illuminate the
238 tank. The light intensity was maintained at 54 lux. Two synchronized high-speed video
239 cameras (HAS-L1, Ditect Co., Tokyo, Japan) were used to record dorsal and side views
240 of the fish simultaneously. (Note that we only used the dorsal views in this study.)

241 An individual *S. marmoratus* starved for at least 24 h was first introduced into
242 the experimental tank and allowed to acclimate for 30 min. An individual *P. major* was
243 then introduced into a PVC pipe (60 mm diameter) with 112 small holes (3 mm
244 diameter) set in the center of the tank, and acclimated for 15 min. The 15-min period
245 was chosen because a preliminary experiment showed that the fish settled down and
246 opercular beat frequency recovered to the basal level within at most 15 min. After the
247 acclimation period, the trial was started by slowly removing the PVC pipe to release the
248 *P. major*. When *S. marmoratus* attacked the *P. major*, we recorded the movements of
249 both predator and prey using the high-speed video cameras. If *S. marmoratus* did not
250 show any predatory movements for 20 min, the trial was ended. Seven *S. marmoratus*
251 were repeatedly used, but each *P. major* was used only once.

252

253 **Analysis of video sequences**

254 Because the vertical displacements of both fishes were negligible, we only used the

255 dorsal video views in our analyses. Before measuring the kinematic and behavioral
256 variables, we noted the kinematic stage in which each prey was captured. The escape
257 response of *P. major* and the predatory strike of *S. marmoratus* were then analyzed
258 frame by frame using Dipp-Motion Pro 2D (Ditect Co., Tokyo, Japan). The CM and the
259 tip of the snout of *P. major*, and the tip of the snout of *S. marmoratus*, were digitized in
260 each frame, and the following variables were calculated:

261 Flight initiation distance: the distance between the predator's snout and the
262 prey's CM at the onset of stage 1 (Fig. 6, D0). Initial orientation ($^{\circ}$): the angle between
263 the line passing through the predator's snout and the prey's CM, and the line passing
264 through the prey's CM and the prey's snout at the onset of the stage 1 (Fig. 6, A0). Turn
265 angle ($^{\circ}$): the angle between the line passing through the prey's CM and the prey's snout
266 at the onset of stage 1, and the line passing through the prey's CM and the prey's snout
267 at the onset of the return tail flip (Fig. 6, A1). Turn duration (s): the time between the
268 onset of stage 1 and the onset of the return tail flip. Predator speed (mm s^{-1}): the
269 cumulative distance the predator's snout moves during the period between the onset of
270 stage 1 and 0.01 s before the onset of stage 1, multiplied by 100.

271 When prey fish did not show escape responses ($n=3$, Fig. 1), the flight
272 initiation distance was regarded as 0. The initial orientation relative to a predator was
273 calculated at the onset of the predator's strike. The predator speed was calculated during
274 the period between the time of capture and 0.01 s before the time of capture.

275

276 **Statistical analyses**

277 Of the 151 digital films recorded, 46 were used for the data analyses. First, fish that
278 were not sufficiently far from the wall (more than one total length) were omitted from

279 the analysis to eliminate possible wall effects (Eaton and Emberley, 1991). Second, only
280 fish that initiated an escape response from a state of rest were used in the analysis (we
281 excluded cases where *S. marmoratus* chased *P. major* that were already swimming).

282 To test the hypothesis that initial orientation affects escape probability, the
283 effects of initial orientation on escape probability were evaluated using a generalized
284 linear mixed model (GLMM) with a binomial error distribution and a logit link function
285 (Zuur et al., 2009). All the fish were used in this analysis ($n=46$). Success and failure of
286 predator evasion were designated as 1 and 0, respectively, and used as the objective
287 variable. Initial orientation, flight initiation distance, and predator speed were
288 considered as explanatory variables; flight initiation distance and predator speed were
289 included in the model because these variables significantly affected escape probability
290 in previous studies (Dangles et al., 2006; Stewart et al., 2013; Walker et al., 2005).
291 Predator ID was also included as a random factor because unknown predator abilities
292 may affect the evasion outcome. The significance of the explanatory variables was then
293 assessed by progressively removing them from the model and comparing the change in
294 deviance using the likelihood ratio test with a χ^2 distribution (LR test). The final model
295 for estimating the escape probability was also determined by progressively removing
296 the explanatory variables when the variables were not significant in the LR test.

297 The second hypothesis, that initial orientation decreases the turn angle and its
298 duration, was evaluated using a linear mixed model (LMM) (Grafen and Hails, 2002;
299 Zuur et al., 2009). Prey fish that survived until the end of stage 1 were used in this
300 analysis ($n=24$, Fig. 1). Turn angle or turn duration was used as the objective variable,
301 and initial orientation was considered as the explanatory variable. Predator ID was also
302 included as a random factor. The significance of the explanatory variable was assessed

303 by the F test.

304 Prey animals can have spatial bias in detecting an attacking predator (e.g., from
305 a sensory blind zone) (Domenici, 2002; Tyrrell and Fernandez-Juricic, 2015). Therefore,
306 we examined whether the initial orientation affected the responsive parameters. Because
307 a majority of the prey (43/46, 93%) showed escape responses, we could not conduct any
308 statistical analysis regarding responsiveness. Instead, we examined whether initial
309 orientation affected the flight initiation distance using a generalized additive mixed
310 model (GAMM) with a normal error distribution and an identity link function (Zuur et
311 al., 2009). The GAMM was used because flight initiation distance is likely to change in
312 response to changes in initial orientation in a non-linear fashion due to the sensory blind
313 zone. All the fish were used in this analysis ($n=46$). Flight initiation distance was used
314 as the objective variable, and initial orientation and predator speed were considered as
315 explanatory variables. Predator ID was also included as a random factor. The
316 significance of the explanatory variables was assessed by the F test. All the analyses
317 were carried out using R 3.3.2 (The R Foundation for Statistical Computing, Vienna,
318 Austria) with the package *lme4* for GLMM and LMM, and the package *gamm4* for
319 GAMM.

320

321 **Acknowledgements**

322 We thank N. Nishiumi, I. Nakamura and A. Matsuo for their help with the experiment,
323 G. N. Nishihara for his advice on the statistical analyses, and K. Tsurui and Y. Iwatani
324 for kindly allowing us to use their high-speed video camera. We also thank Nagasaki
325 Takashima Fisheries Center for kindly providing hatchery-reared red seabream.

326

327 **Competing interests**

328 No competing interests to declare.

329

330 **Author contributions**

331 Y.K. designed the experiment. H.K. collected the data. H.K. and Y.K. analyzed the data.

332 Y.K. wrote the manuscript.

333

334 **Funding**

335 This research received no specific grant from any funding agency in the public,
336 commercial, or not-for-profit sectors.

337

338 **Data availability**

339 Measured variables (initial orientation, flight initiation distance, turn angle, turn
340 duration, and predator speed), predator ID, and evasion outcome from 46 predator-prey
341 interactions are available as supplementary information in Table S1.

342

343 **References**

344 **Arnott, S. A., Neil, D. M. and Ansell, A. D.** (1999). Escape trajectories of the brown shrimp
345 *Crangon crangon*, and a theoretical consideration of initial escape angles from
346 predators. *J. Exp. Biol.* **202**, 193-209.

347 **Bateman, P. W. and Fleming, P. A.** (2014). Switching to Plan B: Changes in the escape tactics
348 of two grasshopper species (Acrididae: Orthoptera) in response to repeated
349 predatory approaches. *Behav. Ecol. Sociobiol.* **68**, 457-465.

350 **Broom, M. and Ruxton, G. D.** (2005). You can run · Or you can hide: Optimal strategies for
351 cryptic prey against pursuit predators. *Behav. Ecol.* **16**, 534-540.

352 **Bulbert, M. W., Page, R. A. and Bernal, X. E.** (2015). Danger comes from all fronts:
353 Predator-dependent escape tactics of túngara frogs. *PLoS ONE* **10**, e0120546.

354 **Camhi, J. M. and Tom, W.** (1978). The escape behavior of the cockroach *Periplaneta*

- 355 *americana* - I. Turning response to wind puffs. *J. Comp. Physiol. A Sens. Neural*
356 *Behav. Physiol.* **128**, 193-201.
- 357 **Camhi, J. M., Tom, W. and Volman, S.** (1978). The escape behavior of the cockroach
358 *Periplaneta americana* II. Detection of natural predators by air displacement. *J.*
359 *Comp. Physiol. A Sens. Neural Behav. Physiol.* **128**, 203-212.
- 360 **Cooper, W. E.** (2006). Risk factors and escape strategy in the grasshopper *Dissosteira*
361 *carolina*. *Behaviour* **143**, 1201-1218.
- 362 **Cooper, W. E., Pérez-Mellado, V. and Hawlena, D.** (2007). Number, speeds, and approach
363 paths of predators affect escape behavior by the balearic lizard, *Podarcis lilfordi*. *J.*
364 *Herpetol.* **41**, 197-204.
- 365 **Cooper, W. E. and Sherbrooke, W. C.** (2016). Strategic escape direction: orientation, turning,
366 and escape trajectories of zebra-tailed lizards (*Callisaurus draconoides*). *Ethology*
367 **122**, 542-551.
- 368 **Corcoran, A. J. and Conner, W. E.** (2016). How moths escape bats: predicting outcomes of
369 predator-prey interactions. *J. Exp. Biol.* **219**, 2704-2715.
- 370 **Dangles, O., Ory, N., Steinmann, T., Christides, J. P. and Casas, J.** (2006). Spider's attack
371 versus cricket's escape: velocity modes determine success. *Anim. Behav.* **72**, 603-610.
- 372 **Dijkgraaf, S.** (1963). The functioning and significance of the lateral-line organs. *Biol. Rev.* **38**,
373 51-105.
- 374 **Dill, L. M.** (1974). The escape response of the zebra danio (*Brachydanio rerio*) I. The
375 stimulus for escape. *Anim. Behav.* **22**, 711-722.
- 376 **Domenici, P.** (2002). The visually mediated escape response in fish : predicting prey
377 responsiveness and the locomotor behaviour of predators and prey. *Mar. Freshwat.*
378 *Behav. Physiol.* **35**, 87-110.
- 379 **Domenici, P.** (2010). Context-dependent variability in the components of fish escape
380 response: Integrating locomotor performance and behavior. *J. Exp. Zool. A Ecol.*
381 *Genet. Physiol.* **313**, 59-79.
- 382 **Domenici, P. and Batty, R. S.** (1997). Escape behaviour of solitary herring (*Clupea harengus*)
383 and comparisons with schooling individuals. *Mar. Biol.* **128**, 29-38.
- 384 **Domenici, P. and Blake, R. W.** (1997). The kinematics and performance of fish fast-start
385 swimming. *J. Exp. Biol.* **200**, 1165-1178.
- 386 **Eaton, R. C. and Emberley, D. S.** (1991). How stimulus direction determines the trajectory of
387 the Mauthner-initiated escape response in a teleost fish. *J. Exp. Biol.* **161**, 469-487.
- 388 **Eaton, R. C., Lee, R. K. K. and Foreman, M. B.** (2001). The Mauthner cell and other
389 identified neurons of the brainstem escape network of fish. *Prog. Neurobiol.* **63**,
390 467-485.

- 391 **Fuiman, L. A.** (1993). Development of predator evasion in Atlantic herring, *Clupea harengus*
392 *L. Anim. Behav.* **45**, 1101-1116.
- 393 **Grafen, A. and Hails, R.** (2002). Modern statistics for the life sciences. Oxford: Oxford
394 University Press.
- 395 **Howland, H. C.** (1974). Optimal strategies for predator avoidance: The relative importance
396 of speed and manoeuvrability. *J. Theor. Biol.* **47**, 333-350.
- 397 **Kasumyan, A.** (2003). The lateral line in fish: structure, function, and role in behavior. *J.*
398 *Ichthyol./Vopr. Ikhtiol.* **43**, S175-S213.
- 399 **Kawabata, Y., Yamada, H., Sato, T., Kobayashi, M., Okuzawa, K. and Asami, K.** (2016).
400 Pelvic fin removal modifies escape trajectory in a teleost fish. *Fish. Sci.* **82**, 85-93.
- 401 **King, J. R. and Comer, C. M.** (1996). Visually elicited turning behavior in *Rana pipiens*:
402 Comparative organization and neural control of escape and prey capture. *J. Comp.*
403 *Physiol. A Sens. Neural Behav. Physiol.* **178**, 293-305.
- 404 **Lefrancois, C., Shingles, A. and Domenici, P.** (2005). The effect of hypoxia on locomotor
405 performance and behaviour during escape in *Liza aurata*. *J. Fish Biol.* **67**,
406 1711-1729.
- 407 **Meager, J. J., Domenici, P., Shingles, A. and Utne-Palm, A. C.** (2006). Escape responses in
408 juvenile Atlantic cod *Gadus morhua* L.: the effects of turbidity and predator speed. *J.*
409 *Exp. Biol.* **209**, 4174-4184.
- 410 **Scharf, F. S., Buckel, J. A., McGinn, P. A. and Juanes, F.** (2003). Vulnerability of marine
411 forage fishes to piscivory: effects of prey behavior on susceptibility to attack and
412 capture. *J. Exp. Mar. Biol. Ecol.* **294**, 41-59.
- 413 **Stewart, W. J., Cardenas, G. S. and McHenry, M. J.** (2013). Zebrafish larvae evade predators
414 by sensing water flow. *J. Exp. Biol.* **216**, 388-398.
- 415 **Tauber, E. and Camhi, J. M.** (1995). The wind-evoked escape behavior of the cricket *Gryllus*
416 *bimaculatus*: Integration of behavioral elements. *J. Exp. Biol.* **198**, 1895-1907.
- 417 **Turesson, H., Satta, A. and Domenici, P.** (2009). Preparing for escape: Anti-predator posture
418 and fast-start performance in gobies. *J. Exp. Biol.* **212**, 2925-2933.
- 419 **Tyrrell, L. P. and Fernandez-Juricic, E.** (2015). Sensory systems and escape behavior. In
420 *Escaping from predators: an integrative view of escape decisions*, (eds. W. E.
421 Cooper and D. T. Blumstein), pp. 322-342. Cambridge: Cambridge University Press.
- 422 **Umeda, K., Ishizuka, T., Yawo, H. and Shoji, W.** (2016). Position- and quantity-dependent
423 responses in zebrafish turning behavior. *Scientific Reports* **6**, 27888.
- 424 **Walker, J. A., Ghalambor, C. K., Griset, O. L., McKenney, D. and Reznick, D. N.** (2005). Do
425 faster starts increase the probability of evading predators? *Funct. Ecol.* **19**, 808-815.
- 426 **Webb, P. W.** (1986). Effect of body form and response threshold on the vulnerability of four

427 species of teleost prey attacked by largemouth bass (*Micropterus salmoides*). *Can. J.*
428 *Fish. Aqua. Sci.* **43**, 763-771.

429 **Webb, P. W. and Skadsen, J. M.** (1980). Strike tactics of *Esox*. *Can. J. Zool.* **58**, 1462-1469.

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

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

433 **Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A. and Smith, G. M.** (2009). Mixed effects
434 models and extensions in ecology with R. New York, USA: Springer.

435

436

437

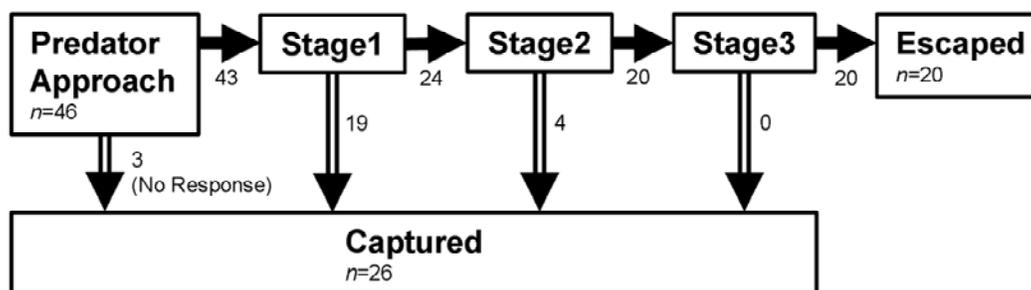
438 Table 1. Comparisons of variables between successful (escaped) and unsuccessful
439 (captured) escapes.

Variable	Escaped	Captured
Initial orientation (°)	79.7±43.5	64.2±51.0
Flight initiation distance (mm)	72.9±30.0	39.3±24.6
Predator speed (mm s ⁻¹)	1536.2±592.2	1343.0±565.5

440

441

442 **Figure captions**

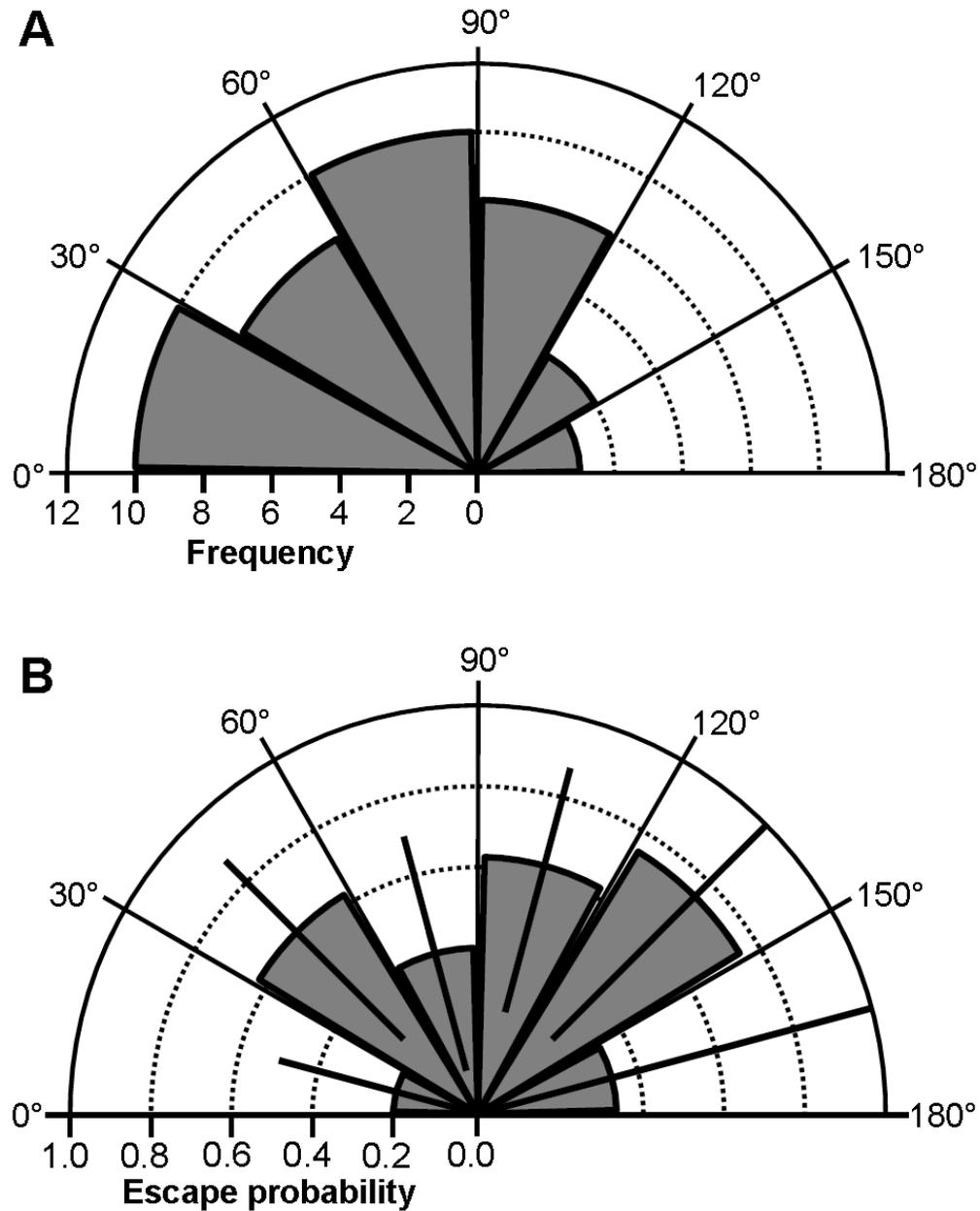


443

444 Fig. 1. Diagram showing the kinematic stages in which the prey were captured.

445

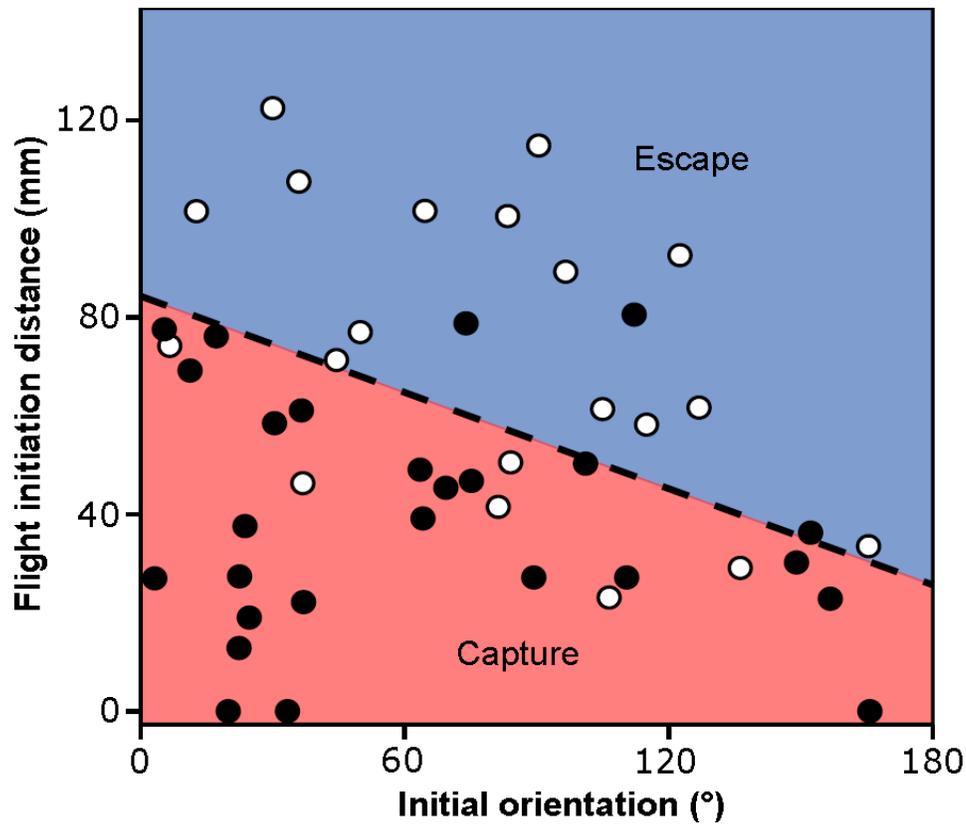
446



447

448 Fig. 2. (A) Frequency distribution of initial orientations. (B) Relationship between
449 initial orientation and escape probability. The error bars represent 95% confidence
450 intervals, estimated by assuming binomial distributions.

451



452

453 Fig. 3. Effect of initial orientation and flight initiation distance on survival probability.

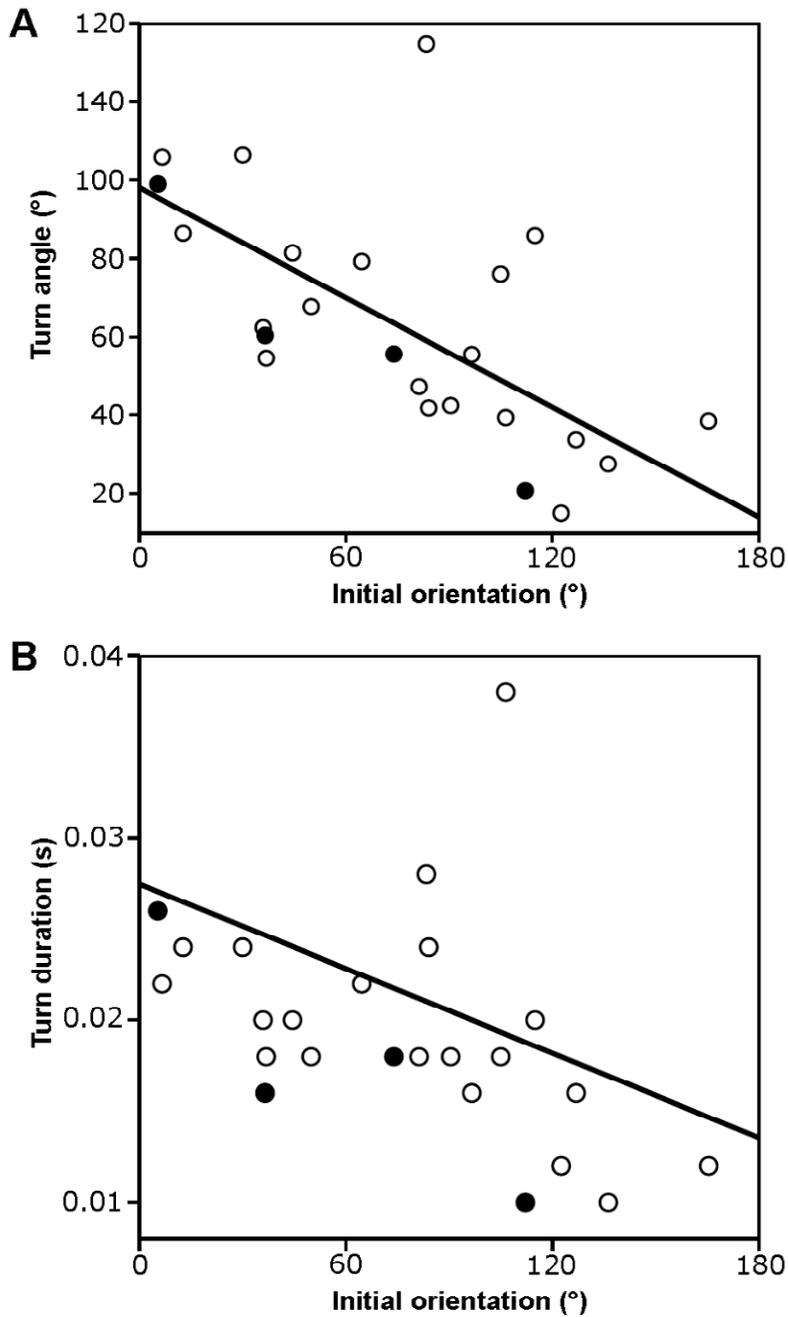
454 Open circles are indicative of successful escape from predator's attack and filled circles

455 are indicative of captured by predator's attack. The dashed line represents the 50%

456 escape probability estimated from the generalized linear mixed model (GLMM). All the

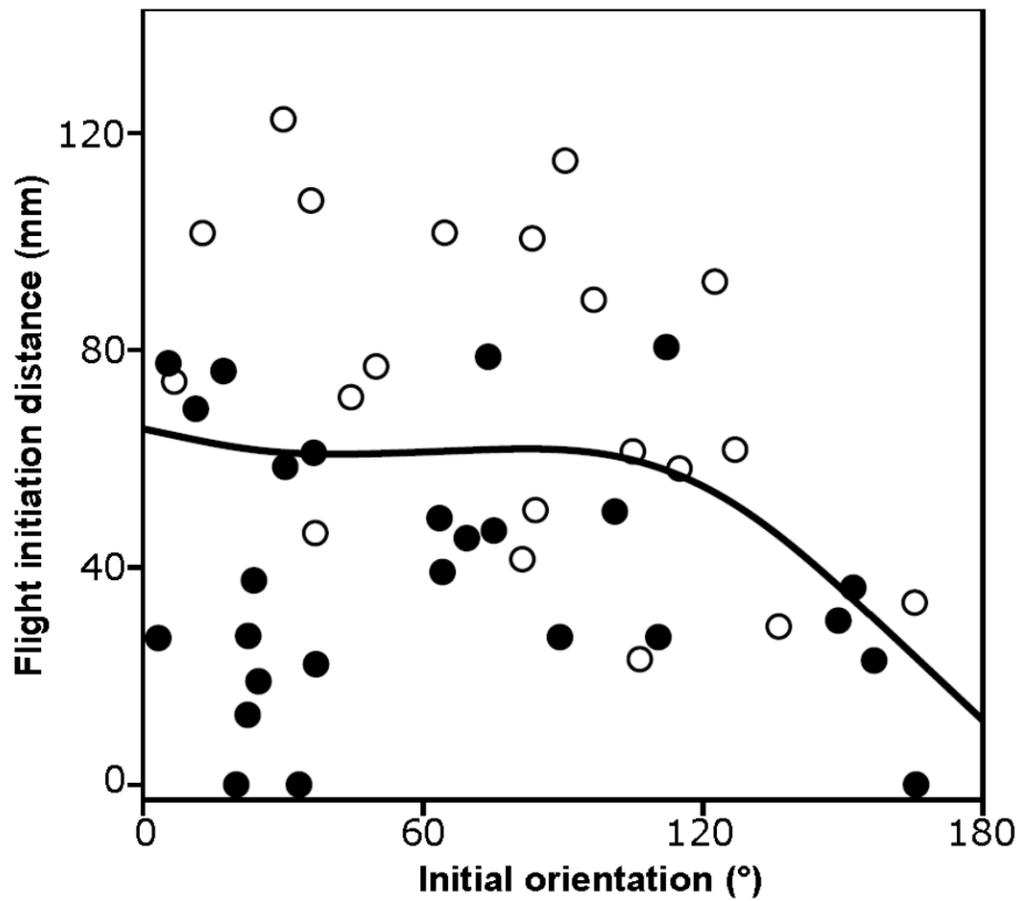
457 prey fish were used in this analysis ($n=46$).

458



459

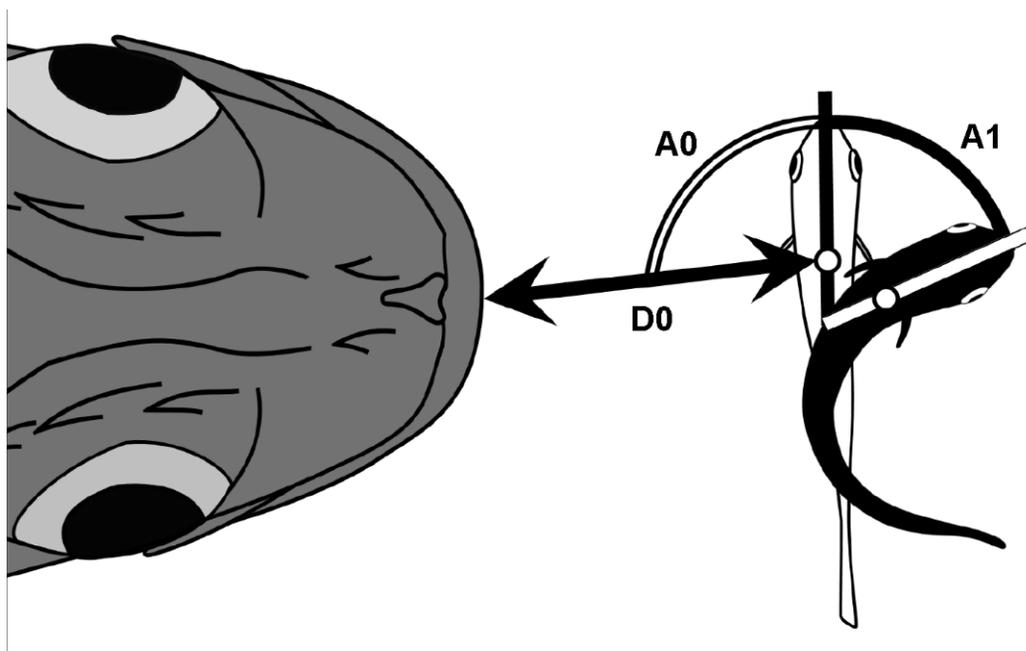
460 Fig. 4. (A) Relationship between initial orientation and turn angle. (B) Relationship
461 between initial orientation and turn duration. Open circles are indicative of successful
462 escape from predator's attack and filled circles are indicative of captured by predator's
463 attack. Prey fish that survived until the end of stage 1 were used in this analysis ($n=24$).



464

465 Fig. 5. Effect of initial orientation on flight initiation distance. The line was estimated
466 by the generalized additive mixed model (GAMM), in which the predator speed was
467 regarded as its mean value (1427 m s^{-1}). All the prey fish were used in this analysis
468 ($n=46$).

469



470

471 Fig. 6. Schematic drawing of measured variables. The position of the prey at the onset
472 of the escape response is shown as an unfilled fish, and the position at the end of stage 1
473 is shown as a filled fish. Unfilled circles represent the prey's center of mass (CM). D0,
474 flight initiation distance; A0, initial orientation; A1, turn angle.

475