Title: Geometrical model explains multiple preferred escape trajectories of fish

Short title: Geometrical model for escape trajectories

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17 **Author contributions:** Y.K. conceived the study; Y.K. and P.D. constructed the theoretical model; Y.K.
 18 and H.A. designed the experiment, Y.K., H.A., H.K., and N.N. conducted the experiment; H.A. and
 19 H.K. digitized the videos; Y.K., K.S., G.N.N., and P.D. conducted statistical analyses; Y.K. wrote the
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22

23 Abstract

24 To evade predators, many prey perform rapid escape movements. The resulting escape trajectory (ET)
 25 – measured as the angle of escape direction relative to the predator’s approach path – plays a major
 26 role in avoiding predation. Previous geometrical models predict a single ET; however, many animals
 27 (fish and other animal taxa) show highly variable ETs with multiple preferred directions. Although
 28 such a high ET variability may confer unpredictability, preventing predators from adopting counter-
 29 strategies, the reasons why animals prefer specific multiple ETs remain unclear. Here, we constructed
 30 a novel geometrical model in which T_{diff} (the time difference between the prey entering the safety zone
 31 and the predator reaching that entry point) is expected to be maximized. We tested this prediction by
 32 analyzing the escape responses of *Pagrus major* attacked by a dummy predator. At each initial body
 33 orientation of the prey relative to the predator, our model predicts a multimodal ET with an optimal
 34 ET at the maximum T_{diff} ($T_{\text{diff},1}$) and a suboptimal ET at a second local maximum of T_{diff} ($T_{\text{diff},2}$). Our
 35 experiments show that when $T_{\text{diff},1} - T_{\text{diff},2}$ is negligible, the prey uses optimal or suboptimal ETs to a
 36 similar extent, in line with the idea of unpredictability. The experimentally observed ET distribution is
 37 consistent with the model, showing two large peaks at 110–130° and 170–180° away from the predator.
 38 Because various animal taxa show multiple preferred ETs similar to those observed here, this
 39 behavioral phenotype may result from convergent evolution that combines maximal T_{diff} with a high
 40 level of unpredictability.

42 **Significance Statement**

43 Animals from many taxa escape from suddenly approaching threats, such as ambush predators, by
 44 using multiple preferred escape trajectories. However, the reason why these multiple preferred escape
 45 trajectories are used is still unknown. By fitting a newly constructed model to the empirical escape
 46 response data, we show that the seemingly complex multiple preferred escape trajectories can arise
 47 from a simple geometrical rule which maximizes the time difference between when the prey enters the
 48 safety zone and when the predator reaches that entry point. Our results open new avenues of
 49 investigation for understanding how animals choose their escape trajectories from behavioral and
 50 neurosensory perspectives.

51

52 **Introduction**

53 When exposed to sudden threatening stimuli such as ambush predators, many prey initiate escape
54 responses that include turning swiftly and accelerating away from the threat. The escape responses of
55 many invertebrate and lower vertebrate species are controlled by giant neurons that ensure a short
56 response time (1). Many previous studies have focused on two behavioral traits that are fundamental
57 for avoiding predation: when to escape (i.e., flight initiation distance, which is measured as the distance
58 from the predator at the onset of escape) and where to escape [i.e., escape trajectory (ET), which is
59 measured as the angle of escape direction relative to the stimulus direction] (2). Previous studies have
60 investigated the behavioral and environmental contexts affecting these variables (3-8), because they
61 largely determine the success or failure of predator evasion (9-13), and hence the fitness of the prey
62 species. A large number of models on how animals determine their flight initiation distances have been
63 formulated and tested by experiments (2). Although a number of models have also been developed to
64 predict animal ETs (4, 14, 15), there are still some unanswered questions about how the variability of
65 the observed ETs is generated.

66 Previous geometrical models predict a single ET that depends on the relative speeds of the
67 predator and the prey (4, 14, 15). However, these simple models do not explain the complex ET
68 distributions reported in empirical studies on various taxa of invertebrates and lower vertebrates
69 (reviewed in ref. 16). Whereas some animals exhibit unimodal ET patterns that satisfy the geometrical
70 models (e.g., ref. 17), many animals show multimodal ETs within a limited angular sector (esp., 90–

180°) (e.g., ref. 4, 5, 18). To explore the discrepancy between the predictions of the models and empirical data, some researchers have hypothesized mechanical/sensory constraints (16, 19) and unpredictability, in line with the idea of a protean response that does not allow predators to adopt counter-strategies (19-21). Although these hypotheses, together with the previous geometrical models, can explain the ET variability within a limited angular sector, the reasons why animals prefer specific multiple ETs still remain unclear.

In previous geometrical models, the prey was assumed to instantaneously escape in any direction, irrespective of the prey's initial body orientation relative to the predator's approach path (hereafter, initial orientation) (4, 14, 15). However, additional time is required for the change of the heading direction (i.e. turn), therefore a realistic model needs to take into account that the predator can approach the prey more closely while the prey is turning (12). Additionally, in previous models, attacking predators were assumed to move for an infinite distance at a constant speed (4, 14, 15). However, the attacks of many real predators, especially ambush ones, end at a certain distance from initial positions of the prey (22-24). Therefore, we constructed a geometrical model that incorporates two additional factors: the time required for the prey to turn and the endpoint of the predator attack. We tested whether our model could predict empirically observed multimodal ETs, using the escape response of the prey fish *Pagrus major* against an approaching dummy predator. The biological implications resulting from the model and experimental data are then discussed within the framework of predator-prey interactions.

90

91 **Model**

92 We revised a previous model proposed by Domenici (15, 25) (Fig. 1A). Other previous models (4, 14)
 93 made predictions that were similar to those of Domenici's model although they used different
 94 theoretical approaches. In Domenici's model, the predator with a certain width (i.e. the width of a
 95 killer whale's tail used as a weapon to catch prey) directly approaches the prey, and the prey (the whole
 96 body) should enter the safety zone before the predator reaches that entry point. In this model, the prey
 97 can instantaneously escape in any direction, and the predation threat moves linearly and infinitely.

98 In our new model (Fig. 1B), two factors are added to Domenici's model: the time required for
 99 the prey to turn and the endpoint of the predator attack. We assume that a prey with a certain initial
 100 orientation β (spanning 0–180°, where 0° and 180° correspond to being attacked from front and behind,
 101 respectively) evades a sudden predation threat. The edges of the safety zone are determined by the
 102 width of the predator gape D_{width} , and the distance between the prey's initial position and the predator's
 103 mouth position at the end of the predator attack D_{attack} . This model is based on the escape response of
 104 the horizontal plane, which is realistic for many fish species as well as invertebrate species that walk
 105 on substrates. Startled fish respond to the attack by turning at an angle α , and the ET results from the
 106 angular sum of α and β . ETs from the left and right sides were pooled and treated as though they were
 107 stimulated from the right side (Fig. S1; See "Definition of Angles" in Materials and Methods section
 108 for details).

The prey can escape from the predator when the time required for the prey to enter the safety zone (T_{prey}) is shorter than the time required for the predator's mouth to reach that entry point (T_{pred}). Therefore, the prey is assumed to optimize the difference between the T_{pred} and T_{prey} (T_{diff}). To incorporate the time required for the prey to turn, T_{prey} was divided into two phases: the fast-start phase, which includes the time for turning and acceleration (T_1), and the constant speed phase (T_2). This assumption is consistent with the previous studies (26-28) and was supported by our experiment (See Fig. S3). Therefore:

$$T_{\text{prey}} = T_1 + T_2 \quad [1]$$

For simplicity, the fish was assumed to end the fast-start phase at a certain displacement from the initial position in any α (D_1 ; the radius of the dotted circle in Fig. 1B) and to move at a constant speed U_{prey} to cover the rest of the distance (toward the edge of the safety zone D_2 , plus the length of the body that is posterior to the center of mass L_{prey}). Because a larger $|\alpha|$ requires further turning prior to forward locomotion, which takes time (26, 29), and the initial velocity after turning was dependent on $|\alpha|$ in our experiment (See Fig. 3B), T_1 is given by a function of $|\alpha|$ [$T_1(|\alpha|)$]. Therefore, T_{prey} can be expressed as:

$$T_{\text{prey}} = T_1(|\alpha|) + \frac{D_2}{U_{\text{prey}}} + \frac{L_{\text{prey}}}{U_{\text{prey}}} \quad [2]$$

T_{pred} can be expressed as:

$$T_{\text{pred}} = \frac{D_3 + D_{\text{initial}}}{U_{\text{pred}}} \quad [3]$$

where D_3 is the projection of the prey's escape path along the edge of the sideways safety zone, D_{initial} is the distance between the prey and the predator at the onset of the prey's escape response (i.e., the flight initiation distance or reaction distance), and U_{pred} is the predator speed, which is assumed to be constant. From equations [2] and [3], T_{diff} can be calculated as:

$$T_{\text{diff}} = \frac{D_3}{U_{\text{pred}}} + \frac{D_{\text{initial}}}{U_{\text{pred}}} - T_1(|\alpha|) - \frac{D_2}{U_{\text{prey}}} - \frac{L_{\text{prey}}}{U_{\text{prey}}} \quad [4]$$

The ET toward the upper-left corner of the rectangular danger zone is calculated as $180 - \arctan(\frac{D_{\text{width}}}{2D_{\text{attack}}})$ ($^\circ$), and thus D_2 and D_3 can be expressed as:

$$D_2 = \begin{cases} \frac{D_{\text{width}}}{2 \sin(\alpha + \beta)} - D_1, \alpha + \beta < 180 - \arctan(\frac{D_{\text{width}}}{2D_{\text{attack}}}) \\ \frac{D_{\text{attack}}}{\cos(180 - \alpha - \beta)} - D_1, \alpha + \beta \geq 180 - \arctan(\frac{D_{\text{width}}}{2D_{\text{attack}}}) \end{cases} \quad [5]$$

$$D_3 = \begin{cases} \frac{D_{\text{width}} \tan(\alpha + \beta - 90)}{2}, \alpha + \beta < 180 - \arctan(\frac{D_{\text{width}}}{2D_{\text{attack}}}) \\ D_{\text{attack}}, \alpha + \beta \geq 180 - \arctan(\frac{D_{\text{width}}}{2D_{\text{attack}}}) \end{cases} \quad [6]$$

From equations [4], [5], and [6],

$$T_{\text{diff}} = \begin{cases} \frac{D_{\text{width}} \tan(\alpha + \beta - 90)}{2U_{\text{pred}}} - \frac{D_{\text{width}}}{2U_{\text{prey}} \sin(\alpha + \beta)} - T_1(|\alpha|) - \frac{D_1}{U_{\text{prey}}} + \frac{D_{\text{initial}}}{U_{\text{pred}}} - \frac{L_{\text{prey}}}{U_{\text{prey}}}, \alpha + \beta < 180 - \arctan(\frac{D_{\text{width}}}{2D_{\text{attack}}}) \\ \frac{D_{\text{attack}}}{U_{\text{pred}}} - \frac{D_{\text{attack}}}{U_{\text{prey}} \cos(180 - \alpha - \beta)} - T_1(|\alpha|) - \frac{D_1}{U_{\text{prey}}} + \frac{D_{\text{initial}}}{U_{\text{pred}}} - \frac{L_{\text{prey}}}{U_{\text{prey}}}, \alpha + \beta \geq 180 - \arctan(\frac{D_{\text{width}}}{2D_{\text{attack}}}) \end{cases} \quad [7]$$

Because the terms $\frac{D_1}{U_{\text{prey}}}$, $\frac{D_{\text{initial}}}{U_{\text{pred}}}$, and $\frac{L_{\text{prey}}}{U_{\text{prey}}}$ are independent of α and β , we can calculate the relative

values of T_{diff} (T_{diff}') in response to the changes of α and β , from D_{width} , D_{attack} , U_{prey} , U_{pred} , and

$T_1(|\alpha|)$ as:

$$T'_{\text{diff}} = \begin{cases} \frac{D_{\text{width}} \tan(\alpha + \beta - 90)}{2U_{\text{pred}}} - \frac{D_{\text{width}}}{2U_{\text{prey}} \sin(\alpha + \beta)} - T_1(|\alpha|), \alpha + \beta < 180 - \arctan\left(\frac{D_{\text{width}}}{2D_{\text{attack}}}\right) \\ \frac{D_{\text{attack}}}{U_{\text{pred}}} - \frac{D_{\text{attack}}}{U_{\text{prey}} \cos(180 - \alpha - \beta)} - T_1(|\alpha|), \alpha + \beta \geq 180 - \arctan\left(\frac{D_{\text{width}}}{2D_{\text{attack}}}\right) \end{cases} \quad [8]$$

Given that the escape success is assumed to be dependent on T'_{diff} , the theoretically optimal ET can be expressed as:

$$\text{The optimal ET} = \underset{\alpha + \beta}{\text{argmax}}(T'_{\text{diff}}) \quad [9]$$

Results

Experimental Results

P. major exhibited a typical C-start escape response (Fig. S1), which consists of the initial bend (stage 1), followed by the return tail flip (stage 2), and continuous swimming or coasting (stage 3) (30, 31). Figure 2 shows the effect of the initial orientation β on the ETs. As was done in previous studies (16, 32, 33), the away (contralateral) and toward (ipsilateral) responses, defined as the first detectable movement of the fish oriented either away from or toward the predator, were analyzed separately. When the initial orientation was small (i.e., the prey was attacked head-on; Fig. 2A; $0^\circ \leq \beta < 30^\circ$), two peaks in the ET distribution were observed: a larger peak at around 100° (away response) and a smaller one at around -80° (toward response). As the initial orientation increases (Fig. 2A; $30^\circ \leq \beta < 60^\circ$), the peak at around -80° disappeared. As the initial orientation further increases beyond 60° , another peak appeared at around 170° (Fig. 2A). When the initial orientation was large (i.e., the prey was attacked from behind; Fig. 2A; $150^\circ \leq \beta \leq 180^\circ$), there were two similar-sized peaks in the ET at around 130°

(toward response), and 180–200° (away response). There were significant effects of initial orientation on the ET in both the away and the toward responses [away: generalized additive mixed model (GAMM), $F=214.81$, $P<0.01$; toward: GAMM, $F=373.92$, $P<0.01$]. There were significant effects of initial orientation on the turn angle α in away and toward responses (Fig. S2; away: GAMM, $F=90.88$, $P<0.01$; toward: GAMM, $F=42.48$, $P<0.01$). In the overall frequency distribution of ETs pooling the data on all initial orientations and both toward and away responses, there were two large peaks at 120–130° and 170–180°, and one small peak at around –80° (Fig. 2C). These 3 peaks were confirmed by the Gaussian mixture model analysis (34), where we fitted 1–9 Gaussian curves to the ETs, and selected the most parsimonious model based on the Akaike Information Criterion (AIC) (Table S1).

There were no significant effects of predator speed on the ET and $|\alpha|$ in either the toward or the away responses (ET, away: GAMM, $F=0.01$, $P=0.93$; ET, toward: GAMM, $F=0.05$, $P=0.82$; $|\alpha|$, away: GAMM, $F=0.01$, $P=0.93$; $|\alpha|$, toward: GAMM, $F=0.05$, $P=0.82$). There were no significant effects of predator speed [slow (from the minimum to the 33.3% quantile): 0.13~0.93 m/s; and fast (from the 66.7% quantile to the maximum): 1.29~1.88 m/s] on the variations of ETs and $|\alpha|$ in all 30° initial orientation bins (Levene's test, $W=0.01\sim3.57$, $P=0.07\sim0.91$).

Parameter Estimation

The distance of the fast-start phase (D_1) was regarded as 15 mm based on the relationship between displacement and velocity of the prey in the experiments (Fig. S3), where the velocity increased up to

about 15 mm of displacement from the initial position, beyond which it plateaus; over the 15 mm displacement from the initial position, there were no significant differences in the mean velocity between any combinations of 3-mm intervals in any 30° $|\alpha|$ bins (Fig. S3; paired t -test with Bonferroni's correction, $P>0.05$). There were significant effects of $|\alpha|$ on the time for a displacement of 15 mm from the initial position (GAMM, $F=70.31$, $P<0.01$) and on the mean velocity during the displacement (GAMM, $F=69.49$, $P<0.01$). However, there were no significant effects of $|\alpha|$ on the time required for a displacement of 15 to 30 mm from the initial position (GAMM, $F=1.52$, $P=0.22$) and on the mean velocity during the displacement (GAMM, $F=0.89$, $P=0.27$). Therefore, the time required for the prey to turn was incorporated into the model by analyzing the relationship between $|\alpha|$ and the time required for a displacement of 15 mm. The mean velocity of the prey during the constant phase U_{prey} was estimated to be 1.04 m s^{-1} , based on the experimental data. Because the cut-off distance might affect the overall results of the study, we have repeated all the statistical analyses (See Tables 1, 2, and the text below for results with a cut-off distance of 15 mm) with cut-off distances of 10 and 20 mm and confirmed that the overall results are insensitive to the changes (Tables S2 and S3).

The relationship between $|\alpha|$ and the time required for a displacement of 15 mm, $T_1(|\alpha|)$, is shown in Fig. 3. The time was constant up to 44° of $|\alpha|$, above which the time linearly increased in response to the increase of $|\alpha|$ (Fig. 3A). In the hierarchical Bayesian model, the lowest widely applicable or Watanabe-Akaike information criterion (WAIC) was obtained for the piecewise linear regression model (Table 1). To understand the possible mechanism of the relationship, the relationship

between $|\alpha|$ and initial velocity after a stage 1 turn, calculated as the displacement per second during the 10 milliseconds (ms) after the turn, was also evaluated (Fig. 3B). The velocity increased in response to $|\alpha|$ up to 46° , beyond which it plateaus. In the hierarchical Bayesian model, the lowest WAIC was obtained for the piecewise linear regression model (Table 1). In both relationships, the regression lines by the piecewise linear model were similar to those by the GAMM, suggesting that the general trends of the relationships were clearly captured by this method. The change points of the two relationships were not significantly different [difference: $1.70 \pm 18.01^\circ$ (mean $\pm$ 95% Bayesian credible intervals)]. These results indicate that fish with a small $|\alpha|$ ($\ll 45^\circ$) can accomplish the stage 1 turn quickly but their velocity after the turn is lower, while fish with an intermediate $|\alpha|$ ($\approx 45^\circ$) spend a longer time on the stage 1 turn, but their velocity after the turn is higher. Fish with a large $|\alpha|$ ($\gg 45^\circ$) spend a still longer time on the stage 1 turn, but their velocity after the turn is similar to that with an intermediate $|\alpha|$ (Fig. 3).

Because we have no previous knowledge about the values of U_{pred} and D_{attack} that the prey regards as dangerous, we have optimized the values from the perspective of the prey using the experimental data (See Materials and Methods for details). Briefly, the optimal values for prey were obtained using the ranking index, where 0 means that the real fish chose the theoretically optimal ET where T_{diff} is the maximum, and 1 means that the real fish chose the theoretically worst ET where T_{diff} is the minimum (e.g., going toward the predator). The result shows that the optimal value of D_{attack} is 35.29 mm and the optimal value of U_{pred} is 1.34 m s^{-1} . Using data from previously published predator-

prey experiments on the same species of prey and predator (12), we show that the estimated D_{attack} value is at the upper limit of the empirical data and the estimated U_{pred} value is higher than the mean of the observed predator speed (Fig. S4). These results suggest that the values independently estimated in the present study are reasonable, and the prey chooses the ETs by estimating the values of D_{attack} and U_{pred} to be higher than their means used by the real predator, likely because an unsuccessful escape can result in death or severe injury.

Comparison of Model Predictions and Experimental Data

Figure 4A plots the relationships between the ET and the relative time difference T_{diff} for different initial orientations β , estimated by the geometrical model; Fig. 4B plots the relationship between the initial orientation and the theoretical ET. Forty percent, 77%, and 94% of observed ETs were within the top 10%, 25%, and 40% quantiles, respectively (0.1, 0.25, 0.40 ranking index) of the theoretical ETs (Figs. 4B and S5). In general, the predicted ETs are in line with the observed ones, where the model predicts a multimodal pattern of ET with a higher peak (i.e., optimal ET) at the maximum T_{diff} ($T_{\text{diff},1}$) and a second lower peak (i.e., suboptimal ET) at the second local maximum of T_{diff} ($T_{\text{diff},2}$). When the initial orientation is $<20^\circ$ (Figs. 4A; $\beta = 15^\circ$, 4B and 5B), the optimal and suboptimal ETs are around 100° (away response) and -100° (toward response), respectively, which is consistent with the bimodal distribution of our experiment (Fig. 2A; $0^\circ \leq \beta < 30^\circ$). At initial orientations in the range 20° – 60° , the suboptimal ET switches from around -100° to 170° (Figs. 4A; $\beta = 45^\circ$, 4B and 5B), although

$T_{\text{diff},2}$ is extremely small compared to $T_{\text{diff},1}$ (Figs. 4A; $\beta = 45^\circ$, 4B and 5B). Accordingly, the second peak (i.e., at around 170°) was negligible in our experimental data (Fig. 2A; $30^\circ \leq \beta < 60^\circ$), even though the fish can potentially reach such an ET (i.e., from such an initial orientation, an 170° ET is within the upper limit of $|\alpha|$, 147°). When the initial orientation is $60\text{--}120^\circ$ (Figs. 4A; $\beta = 75^\circ$ and $\beta = 105^\circ$, 4B and 5B), the optimal ET is $100\text{--}140^\circ$ (gradually shifting from 100° to 140°), and the suboptimal ET is around 170° . These two peaks and the shift of the optimal ET are consistent with the experimental results (Fig. 2A; $60^\circ \leq \beta < 90^\circ$ and $90^\circ \leq \beta < 120^\circ$). The values of the optimal and suboptimal ETs are reversed at initial orientations $>120^\circ$ (Figs. 4B and 5B), as the optimal and suboptimal values become $170\text{--}180^\circ$ and around 140° , respectively (Fig. 4A). These results are again consistent with the bimodal distribution of our experiments (Fig. 2A; $120^\circ \leq \beta < 150^\circ$ and $150^\circ \leq \beta \leq 180^\circ$).

Figure 4C shows the circular histogram of the overall theoretical ETs estimated by Monte Carlo simulation. The theoretical ETs show two large peaks at around $110\text{--}130^\circ$ and $170\text{--}180^\circ$, and one small peak at around -100° (Fig. 4C). This theoretically estimated ET distribution is similar to the frequency distribution of the observed ETs (Fig. 2C); there were no significant differences in the frequency distribution between theoretical and observed ETs in 986 of 1000 simulations (Table 2; two-sample Kuiper test, median $V=0.10$, median $P=0.63$).

To investigate how the initial orientation of the prey modulates the proportion of using the theoretically optimal ET (i.e., where T_{diff} is the maximum, $T_{\text{diff},1}$) compared to using the suboptimal ET (i.e., where T_{diff} is the second local maximum, $T_{\text{diff},2}$), we calculated the optimal ET advantage

255 ($T_{\text{diff},1} - T_{\text{diff},2}$) (Fig. 5A), which represents the difference in the buffer time available for the prey to
 256 escape from the predator, at different initial orientations. The fish chose the optimal and suboptimal
 257 ETs to a similar extent when the optimal ET advantage is negligible (Fig. 5C). For example, when
 258 looking at the optimal ET advantage < 2 ms, where the initial orientation is $0-7^\circ$ and $106-180^\circ$ (46%
 259 of all initial orientations), the proportion of the optimal ET used was only 55% (Fig. 5B and C). On
 260 the other hand, the proportion of the optimal ET used was 78% when the optimal ET advantage is
 261 higher than 5 ms (i.e., when the initial orientation is $17-82^\circ$) (Fig. 5B and C). There was a significant
 262 effect of optimal ET advantage on the proportion of the optimal ET used by fish tested in our
 263 experiments (Mixed-effects logistic regression analysis, $\chi^2 = 11.06$, $P < 0.01$).

264 To investigate the effects of two factors [i.e., the endpoint of the predator attack D_{attack} and the
 265 time required for the prey to turn $T_1(|\alpha|)$] on the predictions of ET separately, we constructed three
 266 additional geometrical models (Figs. S6–S8): a model that includes only D_{attack} , a model that includes
 267 only $T_1(|\alpha|)$, and a null model that includes neither factors (Fig. 1A and ref. 15). In all of these models,
 268 the theoretical ET distributions estimated through Monte Carlo simulations were significantly different
 269 from the observed ET distributions (Table 2; two-sample Kuiper test, median $P < 0.01$). The null model
 270 and the model with $T_1(|\alpha|)$ show unimodal patterns of ET distribution (Figs. S7 and S8). Although the
 271 model with D_{attack} shows a multimodal pattern of ET distribution, the simulation based on this model
 272 does not match the experimental data, likely because of differences in the relative heights of the peaks
 273 (Fig. S6).

274

275 Discussion

276 Our geometrical model, incorporating the endpoint of the predator attack, D_{attack} , and the time required
 277 for the prey to turn, $T_1(|\alpha|)$, to maximize the difference between the prey and the predator in the time
 278 of arrival at the edge of the safety zone, T_{diff} , clearly explains the multimodal patterns of ETs in P .
 279 *major*. Figure 6 shows an example of how multiple ETs result in successful escapes from predators.
 280 Specifically, according to the model, when the prey escapes at 140° or 170° , it will not be captured by
 281 the predator. On the other hand, when the prey escapes along an intermediate trajectory (157°), it will
 282 be captured because it swims toward the corner of the rectangular danger zone to exit it, and therefore
 283 it needs to travel a longer distance than when escaping at 140° or 170° . This example illustrates that
 284 the multimodal patterns of ETs are likely to be attributable to the existence of two escape routes: either
 285 moving sideways to depart from the predator's strike path or moving away from the predator to outrun
 286 it. Interestingly, both components of the predator-prey interaction [i.e., D_{attack} and $T_1(|\alpha|)$] added to the
 287 previous model (15) are important for accurate predictions of the ET distribution because when they
 288 are considered by the model separately, the predictions do not match the experimental data (Figs. S6
 289 and S7; Table 2).

290 Two different escape tactics have been proposed to enhance the success of predator evasion:
 291 the optimal tactic, which maximizes T_{diff} (i.e., the distance between the prey and the predator) (4, 14,
 292 15), and the protean tactic, which maximizes unpredictability to prevent predators from adjusting their

293 strike trajectories accordingly (19-21, 35). Our results suggest that the prey combines these two
 294 different tactics by using multiple preferred ETs. Specifically, when the optimal ET advantage is large
 295 (i.e., when the initial orientation is 20–60°), the prey mainly uses the optimal ET (Figs. 2A and 5).
 296 However, when the optimal ET advantage over the suboptimal ET is negligible (i.e., the initial
 297 orientation is close to 0° or within the range 110–180°), the prey uses optimal and suboptimal ETs to
 298 a similar extent (Figs. 2A and 5). In such cases, the escape trajectory of the prey would be highly
 299 unpredictable for the predator. While the unpredictability at initial orientations near 0° and 180° can
 300 be easily explained by the left-right indecision at orientations nearly perpendicular to the threat (18,
 301 33, 36), yielding ETs that are approximately symmetrical to the axis of the predator attack, the
 302 unpredictability observed at initial orientations near 110–180° is related to the similarly advantageous
 303 choice between escaping with an ET at around 140° or 180°. Interestingly, at initial orientations >120°,
 304 our results show that these two ETs are reached by using toward and away responses, respectively. The
 305 overlap between the ETs of toward and away responses in the overall dataset (Fig. 2) suggests that
 306 toward responses are not "tactical mistakes" of the prey that turns toward a threat, but are simply related
 307 to reaching an optimal or suboptimal ET. These results suggest that the prey strategically adjusts the
 308 use of optimal and protean tactics based on their initial orientation. This allows the prey to have
 309 unpredictable ETs, thereby preventing predators from anticipating their escape behavior, while keeping
 310 T_{diff} large enough to enter the safety zone before the predator reaches it.

311 A relevant question from a perspective of neurosensory physiology is how the animals are

able to determine their ETs within milliseconds of response time. The initial orientation of the prey has been incorporated into various neural circuit models (37-40), but these models assume that prey animals always escape toward 180° (i.e., opposite to the stimulus source), irrespective of the initial orientation. However, the present study shows that animals use suboptimal ETs as well as optimal ETs, and that these ETs may change in a nonlinear fashion, depending on the initial orientation. Thus, we require new neurophysiological models of ETs to understand how neural circuits process the sensory cues of a threatening stimulus, resulting in muscle actions that generate multiple preferred ETs.

Our geometrical model assumes that the prey determines the ETs based on a fixed predator speed. This assumption is supported by the results of our experiments, where the effects of predator speed on the mean and variability of ETs are not significant. Although we did not find any effect of predator speed, it is possible that a speed outside the range we used may affect ETs. Recent studies show that larval zebrafish *Danio rerio* exhibit less variable ETs under faster threats than they do under slower threats (41, 42), and the difference in ET variability between fast and slow threats is dependent on whether the Mauthner cell is active or not (42). Therefore, any differences in the ET variability of the present study compared to previous studies could be related to the different involvement of the Mauthner-cells. Using the conventional geometrical model, Soto *et al.* (14) showed that the choice of ET only matters to a prey when the predator speed is intermediate, because a prey that is much faster than its predator can escape by a broad range of ETs, whereas a prey that is much slower than its predator cannot escape by any ETs (43). The predator speed used in this study is in the range of the

real predator speed in the previous study using the same species of both predator and prey (12). Thus, our results are ecologically relevant, and the prey is likely to have optimized their ETs based on a fixed predator speed, where the choice of ET strongly affects their survival.

The relationship between $|\alpha|$ and the time required for a 15-mm displacement, $T_1(|\alpha|)$, (Fig. 3A) indicates that the time required for a 15-mm displacement is relatively constant up to an $|\alpha|$ of about 45° , while a further change in $|\alpha|$ requires additional time. This relationship is likely to be attributable to the kinematics and hydrodynamics of the C-start escape response, because the initial velocity after the stage 1 turn increases linearly up to about 45° , beyond which it plateaus (Fig. 3B). Interestingly, a recent study on swimming efficiency during acceleration found that efficiency increases linearly with yaw amplitudes up to a certain value, beyond which efficiency plateaus (44).

Our geometrical model may be applicable to ETs in other predator-prey systems. The model assumes that the predator makes an in-line attack toward the prey with a limited attack distance. This assumption is likely to be met in attacks by ambush and stalk-and-attack predators (45), such as frogs (11), spiders (13), and many fish species (12, 22, 23, 46). Conversely, some predators adjust their strike direction before and/or during the attack (47-50). Such cases probably violate the model assumption and might be better modeled by a different predator movement (50, 51). Further empirical measurements of both prey and predator movements should be accumulated to confirm whether and in which cases our model accurately describes real predator-prey behaviors.

Our results represent a major advancement in understanding the basis of the variability in ETs

observed in previous works (reviewed in ref. 16). Our results suggest that prey use multiple preferred ETs to maximize the time difference between itself and the attacking predator, while keeping a high level of unpredictability. The results also suggest that prey strategically adjust the use of protean and optimal tactics with respect to the advantage of the optimal ET over the suboptimal ET. Because multimodal ETs similar to what we observed here have been found in many fish species and other animal taxa (16), this behavioral phenotype may result from convergent evolution in phylogenetically distant animals. From a neurosensory perspective, our findings open new avenues to investigate how the animals determine their ETs from multiple options with specific probabilities, which are modulated by the initial orientation with respect to the threat.

Materials and Methods

Definition of the Angles

The C-start escape response consists of an initial bend (stage 1), followed by a return tail flip (stage 2), and continuous swimming or coasting (stage 3) (30, 31). In line with previous studies (16, 33, 52), we defined directionality (away or toward responses), initial orientation β , turn angle α , and ET $\alpha+\beta$ as follows (Fig. S1). *Directionality*: the away and toward responses were defined by the first detectable movement of the fish in a direction either away from or toward the predator, respectively (16). *Initial orientation* (β): the angle between the line passing through the prey's center of mass [CoM; located at

34% of the total length from the tip of the snout (12)] and the tip of the snout at the onset of stage 1, and the midline of the predator model attacking in a straight line. Initial orientation ranges from 0° (i.e., when the prey is attacked from front) to 180° (i.e., when the prey is attacked from behind). *Turn angle* (α): the angle between the line passing through the CoM and the tip of the snout at the onset of stage 1, and the line passing through the CoM at the onset of stage 1 and the CoM at the end of stage 2. The angles of the away and toward responses are assigned positive and negative values, respectively. *ET* ($\alpha+\beta$): the sum of the initial orientation (β) and the turn angle (α). ET is a circular variable since it can span 360°. Because the experimental data exhibited no asymmetry in directionality (Fisher's exact test, $P=1.00$) and ET distribution (two-sample Kuiper test, $V=0.14$, $P=0.61$), we pooled the ETs from the left and right sides, treating all fish as though they were attacked from the right side (16).

Experiment

We have elicited the escape response of *P. major* [45.33 ± 3.48 mm (mean $\pm$ s.d.) total length, $n=23$] using a dummy predator. The experiment was conducted in a plastic tank (540×890×200 mm) filled with seawater to a depth of 80 mm. The water temperature was maintained at 23.8 to 24.7°C. An individual *P. major* was introduced into a PVC pipe (60 mm diameter) set in the center of the tank and acclimated for 15 min. After the acclimation period, the PVC pipe was slowly removed, and the dummy predator, a cast of *Sebastiscus marmoratus* (164 mm in total length and 30 mm in mouth width), was moved toward the *P. major* for a distance of 200 mm by using a plastic rubber band (Fig. S9).

388 Because the previous work shows that *S. marmoratus* attacks *P. major* using a variable speed
 389 $[1.10 \pm 0.65 \text{ (0.09-2.31) m s}^{-1}$, mean $\pm$ s.d. (range)] (12), we used various strengths of plastic rubber
 390 bands to investigate the effect of predator speed on ET. The fish movements were recorded from above,
 391 using a high-speed video camera (HAS-L1; Ditect Co., Tokyo, Japan) at 500 frames s^{-1} . Each
 392 individual *P. major* was recorded from 5 to 20 times. The recorded videos were analyzed frame by
 393 frame using Dipp-Motion Pro 2D (Ditect Co.). The CoM and the tip of the mouth of *P. major* and the
 394 tip of the predator's mouth were digitized in each frame to calculate all the kinematic variables. The
 395 animal care and experimental procedures were approved by the Animal Care and Use Committee of
 396 the Faculty of Fisheries (Permit No. NF-0002), Nagasaki University in accordance with the Guidelines
 397 for Animal Experimentation of the Faculty of Fisheries and the Regulations of the Animal Care and
 398 Use Committee, Nagasaki University.

399 Because our geometrical model predicts that the initial orientation β and the predator speed
 400 U_{pred} affect the ET and turn angle α , we examined these effects by the experimental data using a
 401 GAMM with a normal distribution and identity link function (53). ET and α were regarded as objective
 402 variables, while predator speed and initial orientation were regarded as explanatory variables and were
 403 modeled with a B-spline smoother. Fish ID was regarded as a random factor. Smoothed terms were
 404 fitted using penalized regression splines, and the amount of smoothing was determined using the
 405 restricted maximum likelihood (REML) method. As was done in previous studies (16, 32, 33), the
 406 away and toward responses were analyzed separately. The significance of the initial orientation and

predator speed was assessed by the F -test. The analysis was conducted using R 3.5.3 (R Foundation for Statistical Computing) with the R package *gamm4*.

Parameter Estimation

To predict the relationship between the ET and the relative time difference T_{diff} in each initial orientation by the geometrical model, we obtained D_{width} , D_{attack} , U_{prey} , U_{pred} , and $T_1(|\alpha|)$. D_{width} was regarded as the mouth width of the dummy predator, which was 30 mm. U_{prey} and $T_1(|\alpha|)$ were directly estimated by analyzing the escape responses of the prey. U_{pred} and D_{attack} were optimized by comparing the model outputs with observed ETs.

Estimation of the Prey's Kinematic Parameters

The relationship between $|\alpha|$ and the time required for a displacement of 15 mm, $T_1(|\alpha|)$, was estimated by piecewise linear regression (54). We used piecewise linear regression rather than a commonly used smoothing method such as GAMM, because the smoothing method does not output the timing of the regression change and thus the biological interpretation of the regression curve is problematic (54). The time required for a displacement of 15 mm was regarded as an objective variable, whereas $|\alpha|$ was regarded as an explanatory variable. Fish ID was included as a covariate in order to take into account potential individual differences in the relationship, $T_1(|\alpha|)$. To detect the possible kinematic mechanism of the relationship $T_1(|\alpha|)$, we also examined the relationship between $|\alpha|$ and initial velocity after the

stage 1 turn, using piecewise linear regression. Initial velocity after the stage 1 turn was regarded as an objective variable, $|\alpha|$ was regarded as an explanatory variable, and fish ID was included as a covariate. A hierarchical Bayesian model with a Markov chain Monte Carlo (MCMC) method was used to estimate these relationships (54, 55). The number of draws per chain, thinning rate, burn-in length, and number of chains were set as 200000, 1, 100000, and 5, respectively. To test the overall fit of the model, the WAIC of the model was compared with those of the null model (constant) and a simple linear regression model. MCMC was conducted using RStan 2.18.2 (Stan Development Team 2019).

Estimation of Predator speed and Endpoint of the Predator Attack

Because we had no previous knowledge about the values of U_{pred} and D_{attack} that the prey regards as dangerous (i.e., the values of U_{pred} and D_{attack} that trigger a response in the prey), we optimized the values using the experimental data in this study. We have input the obtained values of U_{prey} , D_{width} , and $T_1(|\alpha|)$ into the theoretical model. The optimal values were obtained using the ranking index. The ranks of the observed ETs among the theoretical ET choices of 1° increment were standardized as the ranking index, where 0 means that the real fish chose the theoretically optimal ET where T_{diff} is the maximum, and 1 means that the real fish chose the theoretically worst ET where T_{diff} is the minimum. The optimal set of D_{attack} and U_{pred} values was estimated by minimizing the mean ranking index of the observed ETs. The distribution of the optimal ranking index was then fitted to the truncated normal distribution

and was used to predict how the fish chose the ETs from the continuum of the theoretically optimal and worst ETs.

Model Predictions

We input the above parameters [D_{width} , D_{attack} , U_{prey} , U_{pred} , and $T_1(|\alpha|)$] into the model and calculated how the choice of different ETs affects T_{diff} for each initial orientation β . Because there was a constraint on the possible range of $|\alpha|$ [i.e., fish escaping by C-start have a minimum and maximum $|\alpha|$ (26)], the range of $|\alpha|$ was determined based on its minimum and maximum values observed in our experiment, which were 9~147°.

To estimate the overall frequency distribution of ETs that include the data on observed initial orientations, we conducted Monte Carlo simulations. In each observed initial orientation, the ET was chosen from the continuum of the theoretically optimal and worst ETs. The probability of the ET selection was determined by the truncated normal distribution of the optimal ranking index (e.g., the fish could choose theoretically good ETs with higher probability than theoretically bad ETs but the choice is a continuum based on the truncated normal distribution). This process was repeated 1000 times to robustly estimate the frequency distribution of the theoretical ETs. In each simulation run, the frequency distribution of the theoretical ETs was compared with that of the observed ETs using the two-sample Kuiper test (56).

To investigate how the real prey changes the probability that it uses the theoretically optimal

ET or suboptimal ET, we regarded the difference between the maximum of T_{diff} (at the optimal ET) and the second local maximum of T_{diff} (at the suboptimal ET) as the optimal ET advantage, and theoretically estimated the values for all initial orientations. We then examined the relationship between the optimal ET advantage and the proportion of the optimal ET the prey actually chose using a mixed-effects logistic regression analysis (53). Each observed ET was designated as the optimal (1) or the suboptimal (0) based on whether the observed ET was closer to the optimal ET or suboptimal ET. When the prey chose the ET that was more than 35° different from both the optimal and suboptimal ETs, the ET data point was removed from the analysis (these cases were rare: 7%). The choice of ET [optimal (1) or suboptimal (0)] was regarded as an objective variable, while the optimal ET advantage was regarded as an explanatory variable. Fish ID was regarded as a random factor. The significance of the optimal ET advantage was assessed by the likelihood ratio test with χ^2 distribution. The analysis was conducted using R 3.5.3 with the R package *lme4*.

To investigate the effects of two factors [i.e., the endpoint of the predator attack D_{attack} and the time required for the prey to turn $T_1(|\alpha|)$] on predictions of ET separately, we compared four geometrical models: the model that includes both D_{attack} and $T_1(|\alpha|)$, the model that includes only D_{attack} , the model that includes only $T_1(|\alpha|)$, and the null model. Note that the null model is equivalent to the previous Domenici's model (15). In all models, the values of U_{pred} and D_{attack} were optimized using the ranking index. The overall frequency distributions of ETs were estimated through Monte Carlo

simulations, and in each simulation run, the theoretical ET distribution was compared with the observed ET distribution using the two-sample Kuiper test.

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Table 1. Widely applicable or Watanabe–Akaike information criterion (WAIC) for each model in the hierarchical Bayesian models

Relationship	WAIC	Δ WAIC
$ \alpha $ – T_1 relationship		
Piecewise linear	1363.7	0
Linear	1376.7	7.0
Constant	1581.1	217.4
$ \alpha $ –initial velocity after stage 1 turn relationship		
Piecewise linear	–218.1	0
Linear	–205.1	13.0
Constant	–171.5	46.6

$|\alpha|$, absolute value of the turn angle; T_1 , time required for a displacement of 15 mm from the initial position. The best models are shown in bold.

611 Table 2. Comparison of the distribution of escape trajectories (ETs) between the model prediction and
612 experimental data using the two-sample Kuiper test

Model	Median Kuiper's V	Median P	Rate of $P > 0.05$
With both D_{attack} and $T_1(\alpha)$	0.10	0.63	0.99
With D_{attack} and without $T_1(\alpha)$	0.25	< 0.01	0.00
Without D_{attack} and with $T_1(\alpha)$	0.18	< 0.01	0.13
Neither D_{attack} nor $T_1(\alpha)$	0.28	< 0.01	0.00

613 D_{attack} , distance between the prey's initial position and the endpoint of the predator attack; $T_1(|\alpha|)$,
614 relationship between the absolute value of the turn angle and the time required for a 15-mm
615 displacement from the initial position (i.e., the time required for the prey to turn).

Fig. 1. A proposed geometrical model for animal escape trajectories. (A) A previous geometrical model proposed by Domenici (15). The predation threat with a certain width (the tail of a killer whale, represented by the black triangle) directly approaches the prey, and the prey should reach the safety zone (grey area) outside the danger zone (white area) before the threat reaches that point. In this model, the prey can instantaneously escape in any direction, and the predation threat moves linearly and infinitely. (B) Two factors are added to Domenici's model: the endpoint of the predator attack, and the time required for the prey to turn. See the text for details of the definitions of the variables and mathematical formulas.

Fig. 2. Results of the experiments of *Pagrus major* attacked by a dummy predator (i.e., a cast of *Sebastiscus marmoratus*). (A) Circular histograms of escape trajectories (ETs) in 30° initial orientation β bins. Solid lines are estimated by the kernel probability density function. Concentric circles represent 5% of the total sample sizes, the bin intervals are 15° , and the bandwidths of the kernel are 50. (B) Relationship between initial orientation and ET. Different colors represent the away (blue) and toward (red) responses. Solid and dotted lines are estimated by the generalized additive mixed model (GAMM). (C) Circular histogram of ETs pooling all the data shown in A. Solid lines are estimated by the kernel probability density function. Concentric circles represent 5% of the total sample sizes, the bin intervals are 15° , and the bandwidths of the kernel are 50. The predator is approaching from the 0° direction.

Fig. 3. The relationship between the absolute value of the turn angle $|\alpha|$ and time-distance variables. (A) Relationship between $|\alpha|$ and the time required for a displacement of 15 mm from the initial position of the prey. (B) Relationship between $|\alpha|$ and the initial velocity after stage 1 turn. Solid black lines are estimated by the piecewise linear regression model, and red lines are estimated by the generalized additive mixed model (GAMM).

Fig. 4. Model estimates. (A) Circular plots of the time difference between the prey and predator T_{diff} in different initial orientations β . The time difference of the best escape trajectory (ET) was regarded as 10 ms, and the relative time differences between 0 and 10 ms are shown by solid lines. Areas without solid lines indicate that either the time difference is below 0 or the fish cannot reach that ET because of the constraint on the possible range of turn angles $|\alpha|$. Concentric circles represent 3 ms. (B) Relationship between the initial orientation β and ET. Solid and dotted lines represent the best-estimated away and toward responses, respectively. Different colors represent the top 10%, 25%, and 40% quantiles of the time difference between the prey and predator within all possible ETs. (C) Circular histogram of the theoretical ETs, estimated by a Monte Carlo simulation. The probability of selection of an ET was determined by the truncated normal distribution of the optimal ranking index (Fig. S5). This process was repeated 1000 times to estimate the frequency distribution of the theoretical ETs. Colors in the bars represent the away (blue) or toward (red) responses. Black lines represent the kernel probability density function. Concentric circles represent 10 % of the total sample sizes, the bin intervals are 15° , and the bandwidths of the kernel are 50. Circular histogram of the observed ETs (Fig. 2C) is shown in the lower right panel for comparison. The predator is approaching from the 0° direction.

Fig. 5. Analyses of the probability that the prey chooses the optimal vs. suboptimal ETs. (A) The time difference between the prey and predator T_{diff} at the initial orientation β of 75° is shown as an example. We defined the difference between the maximum of T_{diff} (at the optimal ET) and the second local maximum of T_{diff} (at the suboptimal ET) as the optimal ET advantage. (B) Relationship between the initial orientation β and the optimal ET advantage. Large and small arrows in circles represent the optimal and suboptimal ETs, respectively, for each β sectors. (C) Relationship between the optimal ET advantage and the proportion of the optimal ET used by the real prey. Optimal ET and suboptimal ET are designated as 1 and 0, respectively. The line was estimated by the mixed effects logistic regression analysis.

Fig. 6. Schematic drawing showing how multiple escape trajectories (ETs) result in successful escapes from predators. The dash-dotted rectangle represents the danger zone the prey needs to exit in order to escape predation, outside of which is the safety zone. When the prey escapes toward the corner of the rectangular danger zone (ET=157°) to exit it, it needs to travel a relatively long distance and therefore the predator can catch it. On the other hand, when the prey escapes with an ET at 170° or 140°, it covers a shorter distance and can reach the safety zone before the predator's arrival. When the prey escapes with an even smaller ET (90°), it will be captured because the shorter travel distance for the predator overrides the benefits of the smaller turn and shorter travel distance for the prey. When the prey escapes with an even larger ET (190°), it will also be captured, because the prey requires a longer time to turn than if escaping along the 170° ET, whereas the travel distance for both predator and prey is the same as that for the 170° ET. In this example, the initial orientation, flight initiation distance, and the body length posterior to the center of mass were set as 110°, 60 mm and 30 mm, respectively.

683 Table S1. Akaike information criterion (AIC) for 1–9 Gaussian mixture models to estimate the empirical ET
684 distribution

Number of peaks	AIC	Δ AIC
3	2777.1	0.0
4	2781.0	3.9
2	2784.1	6.9
5	2787.1	10.0
6	2791.1	14.0
7	2797.1	20.0
8	2798.9	21.8
9	2799.2	22.1
1	2855.7	78.6

685 The best model is shown in bold.

Table S2. Widely applicable or Watanabe–Akaike information criterion (WAIC) for each model to estimate the relationship between the absolute value of the turn angle and the time required for a displacement of 10 or 20 mm from the initial position

Length of displacement	WAIC	ΔWAIC
10 mm		
Piecewise linear	1239.7	0
Linear	1259.0	19.3
Constant	1524.4	284.7
20 mm		
Piecewise linear	1543.3	0
Linear	1547.0	3.7
Constant	1689.7	146.4

The best models are shown in bold.

Table S3. Comparison of the distribution of escape trajectories (ETs) between the model prediction and experimental data using the two-sample Kuiper test

Distance for the fast-start phase	Median Kuiper's V	Median P	Rate of $P > 0.05$
10 mm			
With both D_{attack} and $T_1(\alpha)$	0.10	0.63	0.99
With D_{attack} and without $T_1(\alpha)$	0.25	< 0.01	0.00
Without D_{attack} and with $T_1(\alpha)$	0.17	< 0.05	0.25
Neither D_{attack} nor $T_1(\alpha)$	0.28	< 0.01	0.00
20 mm			
With both D_{attack} and $T_1(\alpha)$	0.11	0.44	0.96
With D_{attack} and without $T_1(\alpha)$	0.25	< 0.01	0.00
Without D_{attack} and with $T_1(\alpha)$	0.15	< 0.05	0.46
Neither D_{attack} nor $T_1(\alpha)$	0.28	< 0.01	0.00

The distance for the fast-start phase was regarded as either 10 or 20 mm. D_{attack} , distance between the prey's initial position and the endpoint of the predator attack; $T_1(|\alpha|)$, relationship between the absolute value of the turn angle and the time required for a 15-mm displacement from the initial position (i.e., the time required for the prey to turn).

Fig. S1. Schematic drawing of angular variables. *Filled circle* position of the center of mass; *Dotted arrow* approach direction of the dummy predator; S_0 position of the fish at the onset of stage 1, S_1 position at the end of stage 1, S_2 position at the end of stage 2, α turn angle, β initial orientation, $\alpha + \beta$ escape trajectory (ET).

Fig. S2. Relationship between initial orientation β and turn angle α in the experiment. Different colors represent the away (blue) and toward (red) responses. Solid and dotted lines are estimated by the generalized additive mixed model (GAMM).

Fig. S3. Relationship between displacement from the initial position (3-mm intervals: 0–3, 3–6, ..., and 27–30 mm) and mean velocity during the displacement for each turn angle ($|\alpha|$) bin. Unfilled circles denote the mean value for each individual. Different lowercase letters represent significant differences according to the paired *t*-test with Bonferroni's correction ($P < 0.05$). (A) $|\alpha| < 30^\circ$. (B) $30^\circ \leq |\alpha| < 60^\circ$. (C) $60^\circ \leq |\alpha| < 90^\circ$. (D) $|\alpha| \geq 90^\circ$. (E) Mean of the individual mean value for each $|\alpha|$ bin. Vertical dashed line represents the cut-off distance of 15 mm used in this study, and vertical dotted lines represent the other cut-off distances tested in this study (Tables S2 and S3).

Fig. S4. Predator attack parameters. (A) Histogram of the distance between the prey's initial position and the predator's mouth position at the onset of the mouth closing (D_{attack}). (B) Histogram of the speed of the real predator *Sebastiscus marmoratus*. Both figures are based on reanalysis of data from Kimura and Kawabata (12). Vertical dashed blue lines represent the optimal values independently estimated in this study, and vertical dotted red lines represent the mean values of the real predator.

Fig. S5. Histogram of the ranking index, where 0 indicates that the real fish chose the theoretically optimal escape trajectory (ET) and 1 indicates that the real fish chose the theoretically worst ET. The solid line is the density probability function of the truncated normal distribution.

Fig. S6. Estimates of the model with D_{attack} (the distance between the prey's initial position and the endpoint of the predator attack) and without $T_1(|\alpha|)$ (the relationship between the absolute value of the turn angle $|\alpha|$ and the time required for a 15-mm displacement from the initial position, or the time required for prey to turn). (A) Circular plots of the time difference between the prey and predator T_{diff} in different initial orientations β . The time difference of the best escape trajectory (ET) was regarded as 10 ms, and the relative time differences between 0 and 10 ms are shown by solid lines. Areas without solid lines indicate that either the time difference is below 0 or the fish cannot go to that ET because of the constraint on the possible range of $|\alpha|$. Concentric circles represent 3 ms. (B) Relationship between the initial orientation β and ET. Solid and dotted lines represent the best-estimated away and toward responses, respectively. Different colors represent the top 10%, 25%, and 40% quantiles of the time difference between the prey and predator within all possible ETs. (C) Circular histogram of the theoretical ETs, estimated by a Monte Carlo simulation. The probability of selection of an ET was determined by the truncated normal distribution of the optimal ranking index. This process was repeated 1000 times to estimate the frequency distribution of the theoretical ETs. Colors in the bars represent the away (blue) or toward (red) responses. Black lines represent the kernel probability density function. Concentric circles represent 10 % of the total sample sizes, the bin intervals are 15° , and the bandwidths of the kernel are 50. The predator is approaching from the 0° direction.

Fig. S7. Estimates of the model with $T_1(|\alpha|)$ (the relationship between the absolute value of the turn angle $|\alpha|$ and the time required for a 15-mm displacement from the initial position, or the time required for the prey to turn) and without D_{attack} (the distance between the prey's initial position and the endpoint of the predator attack). (A) Circular plots of the time difference between the prey and predator T_{diff} in different initial orientations β . The time difference of the best escape trajectory (ET) was regarded as 10 ms, and the relative time differences between 0 and 10 ms are shown by solid lines. Areas without solid lines indicate that either the time difference is below 0 or the fish cannot go to that ET because of the constraint on the possible range of $|\alpha|$. Concentric circles represent 3 ms. (B) Relationship between the initial orientation β and ET. Solid and dotted lines represent the best-estimated away and toward responses, respectively. Different colors represent the top 10%, 25%, and 40% quantiles of the time difference between the prey and predator within all possible ETs. (C) Circular histogram of the theoretical ETs, estimated by a Monte Carlo simulation. The probability of selection of an ET was determined by the truncated normal distribution of the optimal ranking index. This process was repeated 1000 times to estimate the frequency distribution of the theoretical ETs. Colors in the bars represent the away (blue) or toward (red) responses. Black lines represent the kernel probability density function. Concentric circles represent 10 % of the total sample sizes, the bin intervals are 15°, and the bandwidths of the kernel are 50. The predator is approaching from the 0° direction.

Fig. S8. Estimates of the model that includes neither D_{attack} (the distance between the prey's initial position and the endpoint of the predator attack) nor $T_1(|\alpha|)$ (the relationship between the absolute value of the turn angle $|\alpha|$ and the time required for a 15-mm displacement from the initial position, or the time required for the prey to turn). (A) Circular plots of the time difference between the prey and predator T_{diff} in different initial orientations β . The time difference of the best escape trajectory (ET) was regarded as 10 ms, and the relative time differences between 0 and 10 ms are shown by solid lines. Areas without solid lines indicate that either the time difference is below 0 or the fish cannot go to that ET because of the constraint on the possible range of $|\alpha|$. Concentric circles represent 3 ms. (B) Relationship between the initial orientation β and ET. Solid and dotted lines represent the best-estimated away and toward responses, respectively. Different colors represent the top 10%, 25%, and 40% quantiles of the time difference between the prey and predator within all possible ETs. (C) Circular histogram of the theoretical ETs, estimated by a Monte Carlo simulation. The probability of selection of an ET was determined by the truncated normal distribution of the optimal ranking index. This process was repeated 1000 times to estimate the frequency distribution of the theoretical ETs. Colors in the bars represent the away (blue) or toward (red) responses. Black lines represent the kernel probability density function. Concentric circles represent 10 % of the total sample sizes, the bin intervals are 15° , and the bandwidths of the kernel are 50. The predator is approaching from the 0° direction.

Fig. S9. Sketch of the experimental apparatus for measuring the escape response of prey fish *Pagrus major*.