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The pursuit strategy of predatory bluefish (*Pomatomus saltatrix*)

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A predator's ability to capture prey depends critically on how it coordinates its approach in response to a prey's motion. Flying insects, bats and raptors are capable of capturing prey with a strategy known as parallel navigation, which allows a predator to move directly towards the anticipated point of interception. It is unclear if predators using other modes of locomotion are employing this strategy when pursuing evasive prey. Using kinematic measurements and mathematical modelling, we tested whether bluefish (*Pomatomus saltatrix*) pursue prey fish (*Fundulus heteroclitus*) with parallel navigation. We found that the directional changes of bluefish were not consistent with this strategy, but rather were predicted by a strategy known as deviated pursuit. Although deviated pursuit requires few sensory cues and relatively modest motor coordination, a comparison of mathematical models suggested negligible differences in path length from parallel navigation, largely owing to the acceleration exhibited by bluefish near the end of a pursuit. Therefore, the strategy of bluefish is unlike flying predators, but offers comparable performance with potentially more robust control that may be well suited to the visual system and habitat of fishes. These findings offer a foundation for understanding the sensing and locomotor control of predatory fishes.

1. Introduction

A predator's ability to capture evasive prey depends on its pursuit strategy. A pursuit strategy is determined by the details of a behavioural algorithm that dictates how a predator steers in response to the motion of its target. In engineering, such algorithms are known as guidance laws and are employed in applications such as missile guidance and nautical navigation [1]. Flying predators are capable of the strategy of parallel navigation, where the predator attempts to move directly towards the anticipated point of intersection with the prey [2–6]. It is unknown what pursuit strategies are employed by predators that use different modes of locomotion and occupy different habitats. For these understudied animals, it is unclear what sensory cues and measures of locomotor performance matter to predatory behaviour. The aim of the present study was to test whether bluefish, an aggressive, circumglobal predator found in oceanic and coastal waters, uses parallel navigation when it pursues mummichog, a smaller evasive fish.

Pursuit strategies may be distinguished by kinematic measurements. It is helpful for this purpose to consider the motion of a single point on the body of both the predator and prey and the orientation (α) of the line of sight between them (figure 1*a*). In a simple strategy, pure pursuit, the predator aligns its heading (θ) with the line of sight to produce zero bearing ($\phi = \alpha - \theta = 0$). The curvilinear trajectory that is characteristic of this strategy appears in the motion of a variety of animals for non-predatory behaviours. For example, pure pursuit is used by bats following conspecifics [7], honeybees trained to
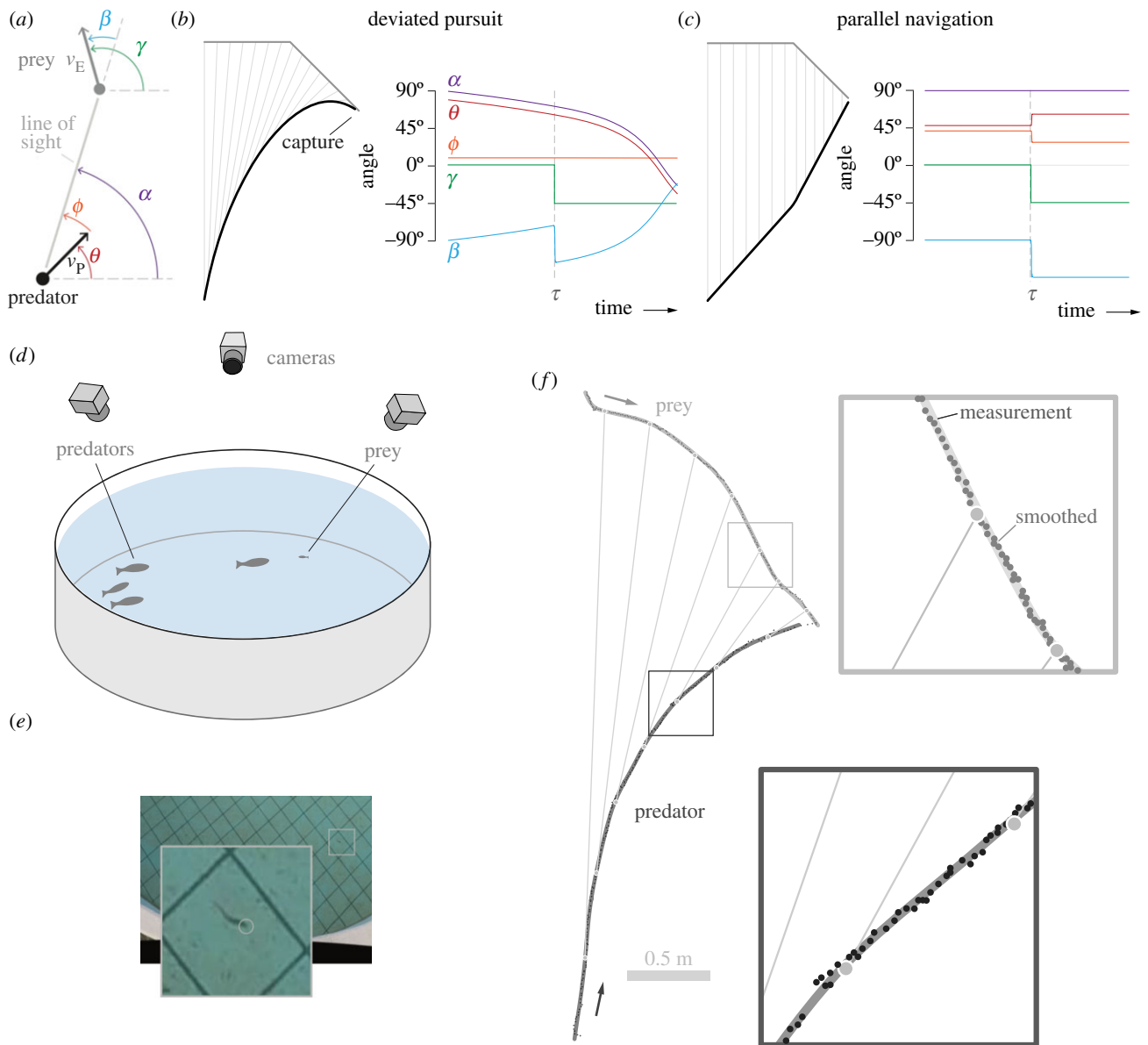
Figure 1. Kinematics of pursuit strategy. (*a*) The motion of a point on the body of a predator (black) and prey (grey) are described relative to the line of sight (light grey line, at angle α) between them. This line serves as a reference for the predator's bearing (ϕ) and the relative heading of the prey (β). Kinematics predicted for (*b*) deviated pursuit (with $\phi' = 10°$) and (*c*) parallel navigation with the line of sight drawn at equal intervals. The kinematic angles for both cases are shown as a function of time given a change (at τ, dashed line) in the prey's heading (γ). (*d*) Predator and prey fish were recorded for two-dimensional kinematics with three high-speed cameras. (*e*) A representative video frame from a recording shows the position of the rostrum (circle) that was selected for each fish. (*f*) The rostral position of predator (black) and prey (grey) are shown for a complete experiment with the range vector highlighted at a regular interval. A smoothing spline was fitted to the trajectory of each animal (heavy line).

track a target [8], and by flies following mates [9] and high-contrast images [10]. Deviated pursuit is similar, but causes the pursuer to seek a non-zero bearing (figure 1*b*), at a particular fixed value known as the bearing offset (ϕ'). Either deviated pursuit or pure pursuit may be implemented by a visually guided predator that merely steers to maintain the prey in its visual field at the bearing offset (figure 1*b*) [11]. The simplicity of bearing control suggests that it may be achieved with rudimentary motor coordination, even when the visual system is poor or compromised.

In contrast to deviated or pure pursuit, parallel navigation allows a flying predator to steer directly to the point of prey interception. When executed correctly, the line of sight is maintained at a fixed angle with respect to a global frame of reference, even if the prey executes a manoeuvre (figure 1*c*). Parallel navigation may be achieved by different guidance laws but generally requires that the predator control

its bearing in response to either the relative speed and heading of the prey or the rate of change in the orientation of the line of sight. A wide diversity of flying predators have demonstrated these abilities by exhibiting parallel navigation, including visually guided dragonflies [3,12] and raptors [5,6], as well as bats [2], which are guided by echolocation. Although these animals are capable of parallel navigation, they may also resort to alternative strategies [5,6], perhaps when sensing or locomotion are compromised.

It is not clear what pursuit strategy is used by predatory fishes. Parallel navigation may offer a more direct route to the prey, but it is unclear if fishes are capable of its requirements for sensing and motor control. At least one species of teleost fish can use parallel navigation to control pitch to intercept a constant-velocity target [13], though it is unclear if that ability translates to an evasive prey that changes its speed and heading. Pure or deviated pursuit offer relatively simple control

3

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but may generate a more circuitous path to the prey and may, therefore, delay capture. In the present study, we tested the predictions of mathematical models of these strategies by measuring two-dimensional trajectories of bluefish and mummichog during pursuit. Our models provided the opportunity to compare the relative performance of the observed strategy against theoretical alternatives for this predator.

2. Material and methods

(a) Kinematics

We recorded video of bluefish (*Pomatomus saltatrix*, Linnaeus, 1766, mean $\pm$ 1 s.d. = 32.6 $\pm$ 4.5 cm, $n = 6$ standard length) as they pursued mummichog (*Fundulus heteroclitus*, Linnaeus, 1766, 7.68 $\pm$ 1.20 cm, $n = 41$). These experiments were performed in a cylindrical (ø = 6.5 m, depth = 0.8 m) outdoor tank (figure 1d,e). This tank was used to hold the bluefish to minimize handling stress and the group behaviour of the fish succeeded in helping elicit feeding. We differentiated individual bluefish in our analysis by body-length measurements from video recordings and each of the 41 experiments analysed featured a unique prey fish. The bluefish that succeeded in capturing the prey was generally a distance of many body lengths from conspecifics during a pursuit and our subsequent analysis showed no evidence of behavioural interactions between the bluefish. Swimming was recorded with three cameras (120 frames s^{-1}, 1920 × 1080 pix, Hero3+ Black, GoPro, San Mateo, CA, USA) directed towards distinct but slightly overlapping regions of the whole tank floor to survey the tank at high resolution. Trajectories were measured for two-dimensional kinematics by manually tracking the position of the rostrum of both fish. This and all acquisition and analysis were performed with custom software developed in MATLAB (v. 2015a, MathWorks, Natick, MA, USA). Further details are described in the electronic supplementary material. All experiments were approved by the University of Florida Animal Care and Use Committee (IACUC no. 201603267) and were performed at the Whitney Marine Laboratory in St Augustine, FL, USA in January 2015.

(b) Mathematical modelling

We formulated predictions for the trajectory of a bluefish according to both parallel navigation and deviated pursuit strategies using a proportional pursuit guidance law. For either strategy, the change in a predator's heading was modelled by the following first-order differential equation:

$$\dot{\theta} = k \sin(\phi + \phi_0) = k \sin(\alpha + \phi_0 - \theta), \qquad (2.1)$$

where k is the proportional gain ($k > 0$) and ϕ_0 is the bearing set-point. The bearing set-point for parallel navigation was treated as a variable that was free to change according to the relative motion of predator and prey, as defined by the following equation [1]:

$$\phi_{0,\text{para}} = \sin^{-1}\left(\frac{\sin \beta}{K}\right), \qquad (2.2)$$

where K indicates the relative speed of the predator ($K = v_\text{P}/v_\text{E}$) and the relative heading satisfies $-\pi < \beta < \pi$. For deviated pursuit, we modelled the bearing set-point as a fixed parameter that was defined as follows:

$$\phi_{0,\text{dev}} = \text{sgn}(\beta)\,\phi', \qquad (2.3)$$

where ϕ' is the bearing offset. Pure pursuit may thus be defined as the special case of deviated pursuit where $\phi' = 0$. The sign of the prey's relative heading indicates whether the prey is headed towards the left ($\text{sgn}(\beta) = 1$) or right ($\text{sgn}(\beta) = -1$) of the line of sight. We tested the pursuit models against our experiments by performing numerical simulations under the conditions of our

experimental measurements. Each simulation used the position and heading of the predator as initial conditions and the measured values of prey position and predator speed. We measured the instantaneous distances between the predicted and measured trajectory and divided those values by the measured path length as a metric of error throughout a measurement. The mean error, therefore, was used to indicate the overall fit of a simulation to a measured trajectory. Similar to the approach used in a recent study [6], we found the duration of each experiment that was accurately described by a mean error up to the threshold value of 1% (detailed in the electronic supplementary material, figure S2a,b). For deviated pursuit, we performed a series of simulations to find the bearing offset that minimized the mean error. No such optimization was performed for parallel navigation, though that strategy treated the bearing set-point as a variable that was adjusted to the instantaneous motion of the prey. In addition to testing strategies with proportional pursuit (equation (2.1)), we performed the same analysis using the proportional navigation guidance law (described in the electronic supplementary material) and arrived at the same findings.

3. Results

We tested pursuit models for bluefish against kinematic measurements. When applying a mean error threshold of 1%, we found that simulations of parallel navigation deviated from our measurements in many cases for the entire duration of an experiment. This strategy was most predictive of the experiments when little steering was required and hence yielded a relatively straight path (figure 2c). By contrast, the deviated pursuit model fitted most of the duration of almost all experiments. As a result, deviated pursuit predicted a duration (1.01 s, $n = 41$) about twice that of parallel navigation (0.49 s, $n = 41$). This difference was highly significant ($p < 0.001$, Kolmogorov-Smirnov (KS)-test) [14]. It was only when we applied a mean error threshold of 4% or higher that the two models matched a similar duration of the experiments (figure 2d). The bearing offset that best fitted the experimental measurements (circular mean, ±95% confidence interval CI = 3.96°, 2.28° − 5.64°, $n = 41$) was significantly different from the zero value characteristic of pure pursuit (figure 2e) [15]. Therefore, our measurements were most consistent with a strategy of deviated pursuit with a small positive bearing offset.

We compared the performance of different strategies by examining the path length of predicted trajectories. We found no significant difference in path length between deviated pursuit and parallel navigation for simulations using measured prey kinematics and predator speed ($p = 0.998$, $n = 41$, KS-test) [14]. Similarly, no significant differences were found for the path length predicted for pure pursuit and deviated pursuit ($p = 0.999$, $n = 41$, KS-test). Therefore, the deviated pursuit that we observed in bluefish offers performance indistinguishable from pure pursuit and parallel navigation for a prey like mummichog (electronic supplementary material, figure S4a,b).

Additional simulations considered the effects of strategy on the pursuit of simulated prey with a single change in heading (e.g. figure 3a) or speed (e.g. figure 3b). Parallel navigation compared most favourably for prey showing a minor change in direction (figure 3c; electronic supplementary material, figure S5b), similar to what we observed in mummichog (figure 2c). Deviated pursuit performed better for large changes in prey direction (e.g. 90°), particularly if this change occurred relatively early in the pursuit. The advantage of
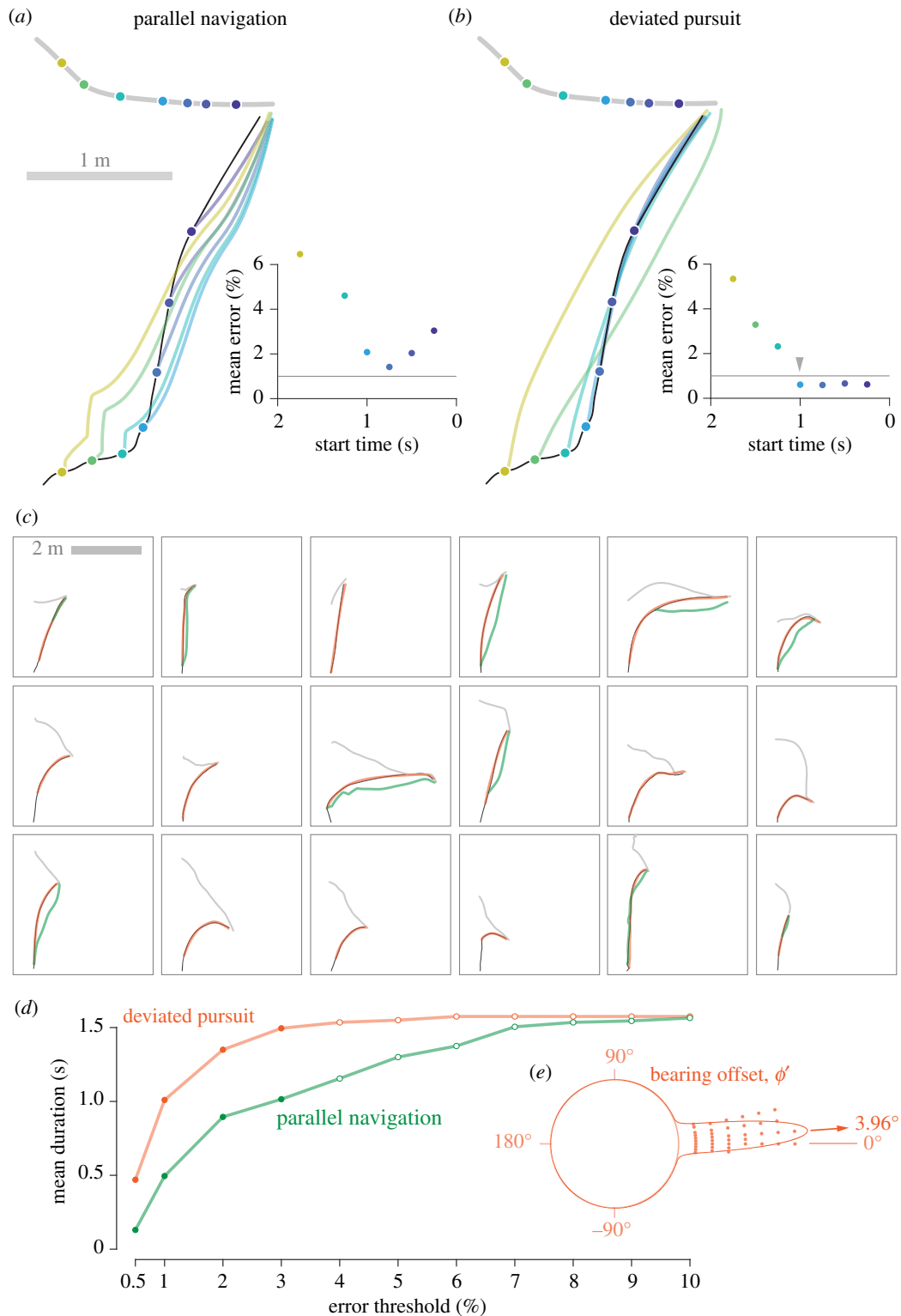
Figure 2. Comparison of pursuit models. (*a,b*) The predicted trajectories for the predator are shown in coloured curves along with the measured trajectories of the prey (grey curve) and predator (black curve) for a representative experiment. The inset graphs indicate the mean error for each predicted trajectory with the 1% threshold highlighted (grey line). At none of the start times during this experiment did (*a*) parallel navigation predict a mean error of less than 1%. (*b*) Deviated pursuit, by contrast, yielded less than 1% at a start time of less than or equal to 1 s (grey arrow). (*c*) A sampling of 18 experiments shows the duration of trajectories predicted for deviated pursuit (orange curve) and parallel navigation (green curve) at a 1% threshold, with the measurements for the predator (black curve) and prey (grey curve). (*d*) The mean duration of all experiments ($n = 41$) predicted for different error threshold values for deviated pursuit (in orange) and parallel navigation (in green). The duration of deviated pursuit was significantly greater (filled circles, $p < 0.05$, KS-test) than parallel navigation for error threshold values of less than 4%. (*e*) The bearing offset that minimized the mean error of the deviated pursuit model was significantly different from zero, according to a fit of a von Mises distribution (curve) to values of individual experiments (circles).

parallel navigation for prey along a straight path could be overcome in cases where the relative speed increased as the predator approached its target (figure 2*d*). For example, if the predator accelerated to a final speed that was 3.75 times

greater than the prey within 1 s from a starting distance of 4 m, then the path length was predicted to be only 2% greater under deviated pursuit than for parallel navigation (electronic supplementary material, figure S7*a*). This acceleration was
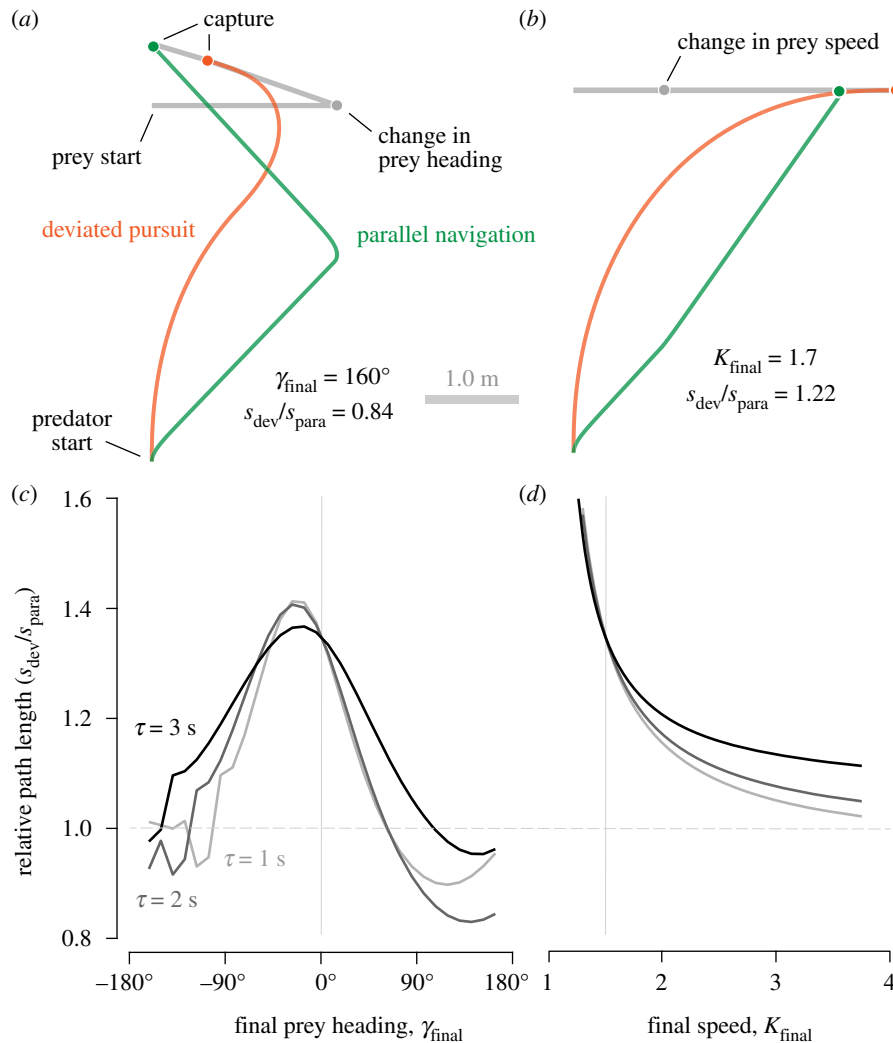
Figure 3. Predictions of predator trajectories for simulated prey. In all simulations, the predator began at a faster speed than the prey ($K_{initial} = 1.5$) and the prey headed at a right angle from the initial line of sight ($\gamma_{initial} = 0°$). The prey then either changed its heading (a,c) or speed (b,d) after some duration (τ). (a,b) Representative simulations show predictions according to the deviated pursuit (orange curve) and parallel navigation (green curve) models for a prey that changes (a) direction or (b) speed ($\tau = 1$ s). See the electronic supplementary material, figure S5 for other examples. (c,d) The relative path length of deviated pursuit (s_{dev}) and parallel navigation (s_{para}) are shown with respect to the (c) final heading and (d) final speed.

similar to the swimming behaviour that we observed in blue-fish (electronic supplementary material, figure S2b), which suggests that any advantage of parallel navigation when pursuing mummichog may have been neutralized by the acceleration of the predator just before capture.

4. Discussion

Our results are consistent with the idea that bluefish use a strategy of deviated pursuit to capture prey (figure 1b). Deviated pursuit replicated most of the duration of bluefish trajectories with a mean error of less than 1% (figure 2c) and consistently predicted a longer duration for mean errors of less than 4% (figure 2d). Our modelling results suggest that bluefish overcome the strategic disadvantages inherent to deviated pursuit by accelerating as they approach their prey.

We used mathematical models to explore how the relative motion between predator and prey affects the predator's path length with simulated prey. Consistent with prior theory, parallel navigation showed a substantial advantage when the prey followed a straight path at constant speed, particularly when directed at a right angle from the predator's

initial position (figure 3c). However, the advantage of parallel navigation subsided when the relative speed increased over time (figure 3b,d), which was exhibited by bluefish (electronic supplementary material, figures S2b and S3). This effect, created by predator acceleration, explains why the deviated pursuit of bluefish showed a comparable path length as parallel navigation for mummichog (electronic supplementary material, figure S4b). Deviated pursuit was also superior to parallel navigation for highly evasive simulated prey, which showed a path length that was nearly 20% shorter (figure 3d). Therefore, deviated pursuit can offer either a comparable or superior path length to parallel navigation, depending on the relative motion of predator and prey.

We found no evidence that bluefish use parallel navigation to pursue evasive prey. This is in contrast to the diversity of flying predators (detailed in Introduction) capable of this strategy. Although raptors can move according to parallel navigation [4,5], Brighton et al. [6] found that the variety of trajectories of peregrine falcons are more generally consistent with a guidance law (proportional navigation) than a particular strategy. If this is true for other flying predators, then our results suggest that bluefish coordinate their pursuits in a fundamentally different

manner. Bluefish moved with consistent strategy (deviated pursuit), irrespective of the guidance law (proportional navigation or proportional pursuit) used to model the behaviour (electronic supplementary material, figure S6). This finding suggests that bluefish use either the bearing (for proportional pursuit) or bearing rate (for proportional navigation) as a cue to control steering.

The execution of a strategy or guidance law depends on the sensory ecology and integration of sensory cues by the predator. In dragonflies, the substantial neuronal processing required for pursuit suggests a capacity to formulate internal models to a degree previously only attributed to mammals [3]. Assisting pursuit is the ability of bats [2], dragonflies [12] and raptors [4,5] to turn their heads and thereby stabilize the position of the prey with respect to sensory organs to some degree independent of body motion. Fish have no such ability, but rather oscillate their cranium and hence their visual field while swimming to an extent that is only partially offset by saccades of the eye [16]. In addition, aquatic environments commonly challenge vision by reducing contrast in turbid water or darkened habitats. High turbidity reduces piscivorous encounter rates in other species of predator fishes [17,18]. Poor contrast may therefore render parallel navigation untenable or challenge the capacity for proportional navigation. Deviated pursuit may be achieved by steering to maintain the prey at a relatively stable position in the visual field. These relatively modest requirements for sensing and motor control suggest that deviated pursuit offers a more robust strategy than parallel navigation. One advantage to deviated pursuit is that it affords an ability to accelerate towards the prey up to the time of capture without large adjustments to its heading, as we found for bluefish (figure 3b,d). Therefore, deviated pursuit is both robust and capable of generating performance comparable to parallel navigation.

Summary

Bluefish move with kinematics that are consistent with a strategy of deviated pursuit with a small positive offset angle when pursuing mummichog. This strategy is indistinguishable from pure pursuit and parallel navigation in terms of the path length of the trajectory. However, deviated pursuit has more modest requirements for sensing and motor control than does parallel navigation. In addition, deviated pursuit can provide superior performance for evasive prey. Therefore, bluefish employ a strategy that is robust and appears well-suited to their sensory biology and locomotor system. These results have the potential for offering a basis for understanding pursuit strategy of predatory fishes.

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