

## SHORT COMMUNICATION

## Pursuit predation with intermittent locomotion in zebrafish

Alberto P. Soto\* and Matthew J. McHenry

## ABSTRACT

The control of a predator's locomotion is critical to its ability to capture prey. Flying animals adjust their heading continuously with control similar to guided missiles. However, many animals do not move with rapid continuous motion, but rather interrupt their progress with frequent pauses. To understand how such intermittent locomotion may be controlled during predation, we examined the kinematics of zebrafish (*Danio rerio*) as they pursued larval prey of the same species. Like many fishes, zebrafish move with discrete burst-and-coast swimming. We found that the change in heading and tail excursion during the burst phase was linearly related to the prey's bearing. These results suggest a strategy, which we call intermittent pure pursuit, that offers advantages in sensing and control. This control strategy is similar to perception and path-planning algorithms required in the design of some autonomous robots and may be common to a diversity of animals.

**KEY WORDS:** Pursuit–evasion, Sensorimotor control, Burst-and-coast, Sensing, Strategy

## INTRODUCTION

Successful predation requires an ability to sense and move toward prey. Models of directional control developed for the navigation of airplanes and missiles (Shneydor, 1998) are predictive of the trajectories of flying insects (Olberg et al., 2007; Fabian et al., 2018), bats (Ghose et al., 2006) and raptors (Kane and Zamani, 2014; Kane et al., 2015; Brighton et al., 2017). However, the rapid and continuous motion of these aerial predators is unlike the intermittent locomotion exhibited by a broad diversity of animals (Paoletti and Mahadevan, 2014; Gleiss et al., 2011). Many fishes move through their environment with discrete bouts of burst-and-coast swimming, and it is unclear how this intermittent locomotion is controlled during prey pursuit. Therefore, our present aim was to determine the pursuit strategy of zebrafish [*Danio rerio* (Hamilton 1822)] when chasing evasive prey.

Pursuit strategy has been investigated in biological systems by measurements of the predator's trajectory during prey pursuit. The two pursuit strategies commonly observed are pure pursuit and interception (Moore and Biewener, 2015; Nahin, 2007), which may be distinguished by measurements of the bearing ( $\phi$ ). This angle is defined as the radial position of the prey relative to the predator's direction of motion or heading (Fig. 1A). In pure pursuit, the bearing is maintained near zero (Fig. S2A), as the predator maneuvers to align its heading with the instantaneous position of the prey. An interception strategy instead guides the predator toward

the point of collision with a bearing angle that considers the heading and speed of the prey. Some predators achieve interception through a guidance law known as proportional navigation (Kane and Zamani, 2014; Kane et al., 2015; Brighton et al., 2017; Fabian et al., 2018), where the turning rate is proportional to the rotation rate of the line-of-sight angle ( $\theta + \phi$  in Fig. 1A). This strategy depends on the rates of relative motion between the animals and offers a near-optimal path to capture (Shneydor, 1998).

It is unclear how our understanding of pursuit strategy in aerial predators relates to the behavior of fishes that move intermittently. Bluefish pursue evasive prey with a strategy similar to pure pursuit (McHenry et al., 2019), but they swim much faster than the prey with continuous motion that is similar to aerial predators. In contrast, some running insects adjust their heading toward live prey with frequent pauses (Gilbert, 1997). In the present study, we considered whether the burst-and-coast swimming of zebrafish is more similar to a bluefish or a running insect as they pursue larvae of the same species.

## MATERIALS AND METHODS

## Predation experiments

Predation experiments were performed with adult zebrafish predators ( $1.49 \pm 0.43$  cm, mean  $\pm$  s.d. standard length,  $N=38$ ) and larval zebrafish prey (5–13 days post-fertilization,  $N=31$ ). After 10 min. in an experimental predation arena (Fig. S1), a divider between the fish was removed and recording proceeded until the predator either captured or otherwise ceased pursuing the prey. Using a high-speed video camera ( $500$  frames  $s^{-1}$ ), we recorded the predator and prey from a dorsal perspective. Numerous ( $N=31$ ) active chase sequences were recorded over a variable duration.

All experiments were conducted in accordance with the University of California, Irvine's Institutional Animal Care and Use Committee (protocol AUP-17-012).

## Experimental setup

Our experimental setup allowed for the filming of predator–prey interactions (Fig. S1) to investigate the pursuit strategy of zebrafish. We used a high-speed video camera (FASTCAM Mini AX100, Photron, San Diego, CA, USA,  $1024 \times 1024$  pixels configured with a macro lens, Micro-Nikkor 105 mm,  $f/2.8$ , Nikon Inc., Melville, NY, USA). To visualize the predator and prey with high contrast, three infrared (IR, 940 nm) LED panels were placed below a translucent white acrylic diffuser, which was placed below the predation arena. A white LED panel placed above the arena provided visible illumination.

## Data processing and analysis

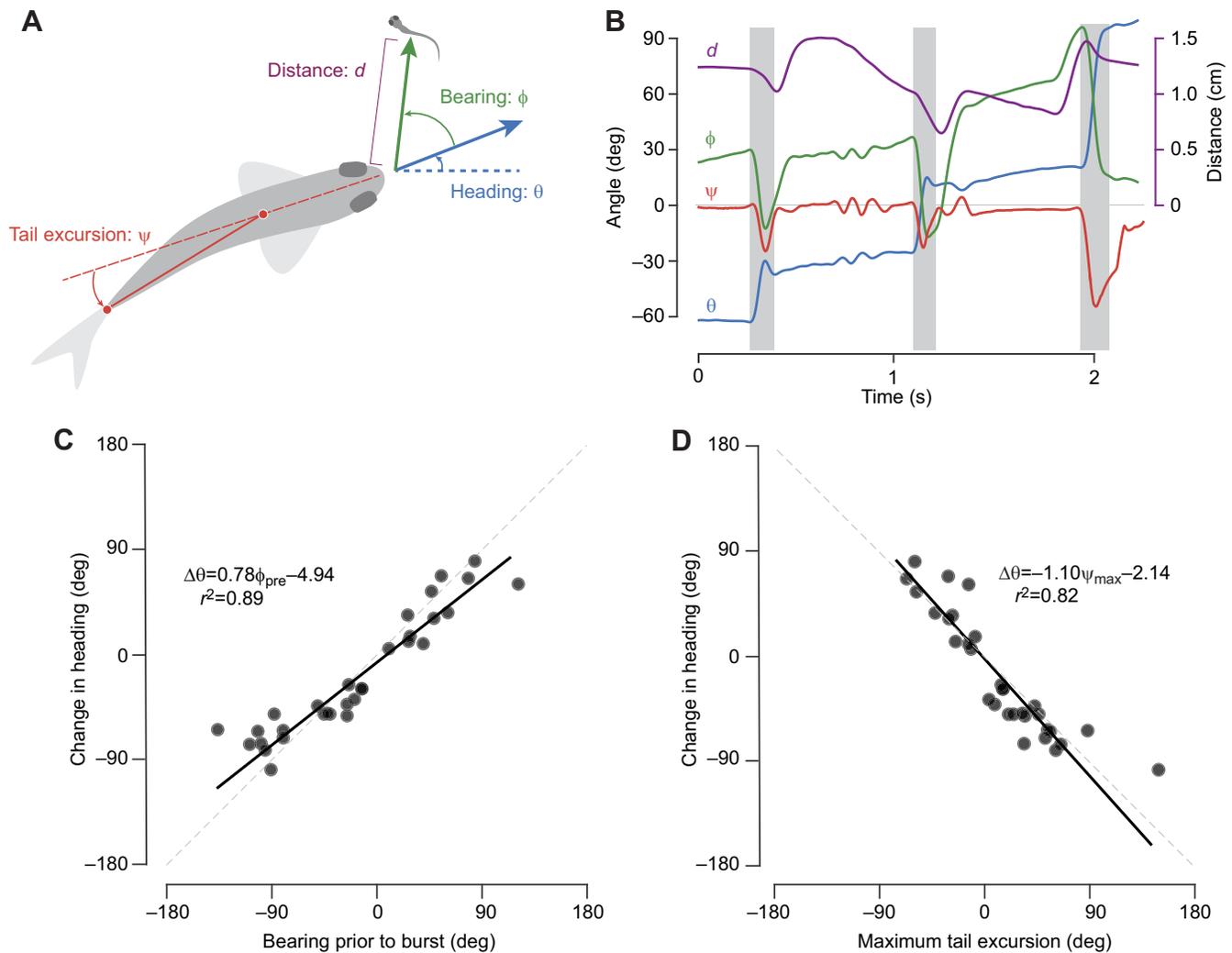
The prey's centroid position and the predator's body midline were acquired through automated image processing of our recordings. This procedure, and all data analyses, were performed by custom programming within MATLAB (v.2014b, MathWorks, Natick, MA, USA, Fig. S2C; see 'Acquisition of kinematics' for details). For each active chase, we identified every burst phase by high rates

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**Fig. 1. Prey pursuit with intermittent locomotion.** (A) The predator's heading ( $\theta$ ) is defined relative to the global frame of reference, the bearing ( $\phi$ ) is defined with respect to heading, and the tail excursion ( $\psi$ ) is the angular deviation between the predator's trunk and the position of the caudal peduncle. (B) Representative measurements of these variables through time, with tail beats (gray bars) during the burst phase of the predator's motion. (C) The change in heading during a tail beat relative to the bearing angle before a burst with a geometric mean slope of 0.78 (solid line, slope 95% CI=0.68–0.88,  $N=31$ ), shown relative to a slope of unity (dashed line). (D) The relationship between the change in heading and maximum tail excursion during tail beats (solid line, slope 95% CI=–1.27 to –0.92,  $N=31$ ), shown relative to a slope of –1 (dashed line).

of change in the predator's heading, and the duration between consecutive bursts was defined as the coast phase (Fig. S2B). To control for variation in chase duration, we randomly selected a single burst from each sequence for further analysis (see Fig. S3 for complete dataset). To assess the predator's pursuit strategy, we considered how the heading change ( $\Delta\theta$ ) during a tail beat was related to the tail excursion ( $\psi$ ) and the bearing (Fig. 1A) by geometric mean regression.

#### Acquisition of kinematics

Our software employed the image processing method known as blob analysis. This approach requires the conversion of grayscale images into binary images by defining a threshold intensity value that partitions dark and light pixels, designated as background and foreground, respectively. The resulting image segmentation technique generates 'blobs' of connected pixels from which features (e.g. centroid and area) may be calculated. After thresholding, the predator's body was distinguished as the largest blob in each frame and its centroid position was recorded. The high

spatial resolution of our experimental setup combined with the size differential of the predator and prey allowed for automated blob analysis for both fish and midline tracking of the predator (Fig. S2).

Our software automatically tracked the midline of the predator fish. This used an input reference image for background subtraction and applied a local thresholding technique ('adapthresh' function in MATLAB). The resulting binary image described the shape of the fish's body, which we refined with morphological operations to fill holes and connect any gaps with neighboring blobs. The prey fish blob was manually selected in the first video frame and subsequently identified by its area and proximity to the previous frame's blob. For each frame, we measured the blob's area and identified its center. The predator blob was identified by a similar procedure and its midline was extracted. The midline was identified by distance mapping, which encodes a value for each pixel of the blob according to its distance to the nearest background pixel. We applied distance mapping along the rows and columns of the binary image, and the resulting maps were concatenated to produce the set of unique pixels that define the predator's midline. For kinematic

analysis, the raw midline coordinates for each video frame were smoothed with the 'loess' method, a locally weighted polynomial regression. We extracted several positions along the predator's midline to compute its heading, center-of-mass velocity, and angular position of the caudal peduncle and fin. The final result was a kinematic dataset for the prey's body and the predator's midline that was obtained automatically.

## RESULTS AND DISCUSSION

We found that zebrafish predators pursued prey with intermittent burst-and-coast swimming. These predators oriented and advanced toward prey during the burst phase, which consisted of a single tail beat. Each burst served to accelerate the predator and induce changes to the predator's heading in a direction that generally reduced the prey's absolute bearing (Fig. 1B). These heading changes were proportional to the bearing prior to the burst (Fig. 1C), but not to the angular velocity of bearing (Fig. S4), and with a slope that was significantly less than unity. This result indicates that the predators tended to yaw slightly less than necessary to orient their swimming directly toward the prey and were driven by tail beats associated with large bearing angles (Fig. S3A).

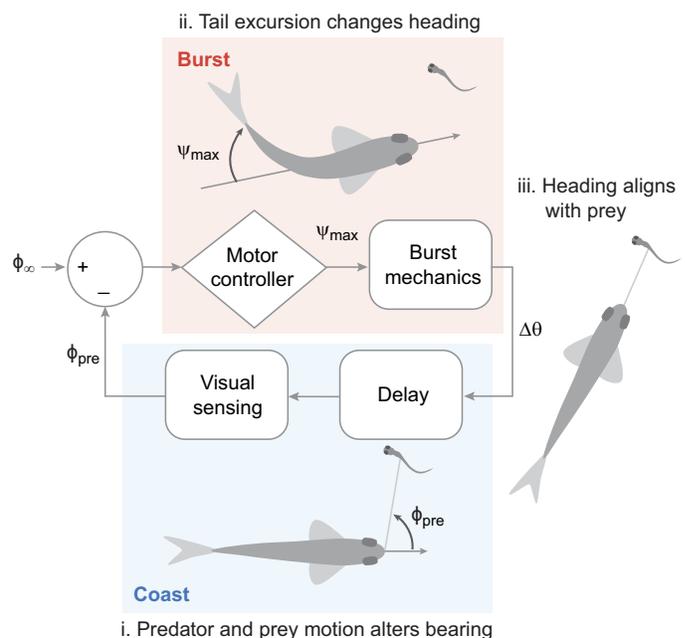
Predators changed their heading during a burst with individual tail beats characterized by a large-amplitude bend of the tail. Occasional periods of continuous, low-amplitude tail beating did not result in a net change in heading (Fig. S2B, blue bar). We found that the maximum excursion of the tail during a burst was linearly related to the change in heading (Fig. 1D). Because of the linear relationship between bearing and the change in heading, the tail excursion was also proportional to the prey's bearing. Therefore, predatory zebrafish modulated their tail beating during a burst in proportion to the prey's bearing at the end of the coast phase. The coast phase lasted about one-third of a second ( $0.32 \pm 0.19$  s,  $N=31$ ) and this duration did not correlate with the distance to the prey at either the onset or the end of coasting (Fig. S5). These kinematic patterns suggest an elegant model of prey targeting control by zebrafish, which we call intermittent pure pursuit.

Pure pursuit may be the best strategy for animals that move intermittently. While interception requires that the predator adopt a heading that depends on the velocity of both animals, pure pursuit depends merely on the angular position of the prey. The intermittent motion of zebrafish yields discrete bursts in angular velocity with little to no change in between (Fig. S2B), similar to the high angular velocity maneuvers of houseflies (Wagner, 1986). In general, the prey type and its behavior also affect the input signals available to the predator (Combes et al., 2013). Larval zebrafish execute rapid escape responses and are often stationary before initiating an escape (Stewart et al., 2013). These discrete signals are therefore unlikely to provide the input necessary for predatory zebrafish to implement an interception strategy. This is in striking agreement with pursuit of live prey in tiger beetles (Gilbert, 1997) and in contrast to continuous pure pursuit (Haselsteiner et al., 2014; Land and Collett, 1974; Gries and Koeniger, 1996), in which pursuers continuously receive input signals and, after some inherent delay, reactively maneuver toward the target based on their feedback controller. A rigorous test of the prey's influence on the predator's pursuit strategy would benefit from experiments that employ a controlled artificial prey (see e.g. Mischiati et al., 2015).

Intermittent locomotion offers a number of advantages over continuous motion. A broad diversity of organisms, from protozoans to mammals, interrupt their forward progress with pauses (Kramer and McLaughlin, 2001). These interruptions can offer energetic benefits that serve to reduce the cost of transport in

flying and swimming animals (Paoletti and Mahadevan, 2014; Gleiss et al., 2011; Rayner et al., 2001; Bianco et al., 2011; Videler et al., 1983; Weihs, 1974; Fish et al., 1991). Spiders dramatically reduce rapid burst activity to recover from depletion of phosphagens (Prestwich, 1988a,b). Interruptions also provide a regular opportunity for enhanced sensing by reducing interference from self-motion (Kramer and McLaughlin, 2001). These regular opportunities for sensing aid in the ability of tiger beetles to relocalize live prey during pursuit (Gilbert, 1997). In many species of fish, tail beating causes the head to yaw, which rotates the visual field to an extent that can be challenging to compensate with saccades of eye rotation (Hermann and Constantine, 1971). In this respect, fishes are at a disadvantage relative to aerial predators such as dragonflies (Olberg et al., 2007), bats (Ghose and Moss, 2003) and raptors (Kane et al., 2015), which move their neck to stabilize the head with respect to a target. Self-motion in fishes may also interfere with modalities other than vision. For example, the flow-sensitive lateral-line system reduces its sensitivity through efferent activation during tail beating (Lunsford et al., 2019; Roberts and Russell, 1972), presumably as a means of differentiating self-induced flows from external stimuli.

The coast phase additionally offers ample time for the nervous system to process complex stimuli and to formulate the motor commands in response. Visual processing has been shown to limit the speed of prey pursuit in some aerial predators and may require high-level cognitive ability to overcome (Lin and Leonardo, 2017; Mischiati et al., 2015). Similar pauses in motion are common in the design of robots to allow for the computational time required for path planning. A pause offers the opportunity for enhanced sensing in a robot through reductions in self-motion and electromagnetic noise generated by motors (Penin et al., 2019; Zhong et al., 2018).



**Fig. 2. Control diagram of intermittent pure pursuit in a fish predator.** (i) A non-zero bearing may be generated by the motion of the predator or prey during the coast phase. At the end of coasting, the bearing ( $\phi_{pre}$ ) is compared with a desired bearing ( $\phi_{des}$ ) and (ii) the motor controller generates a tail beat with maximum tail excursion ( $\psi_{max}$ ). (iii) The tail excursion during the burst phase induces a change in heading ( $\Delta\theta$ ) that causes the predator to align its heading with the prey.

Our experimental results are consistent with the idea that intermittent pure pursuit offers advantages for sensorimotor control. Our measurements support a control model where zebrafish visually locate the position of prey during the coast phase and then execute a tail beat using feed-forward motor commands during the burst phase (Fig. 2). The intensity of these commands may be proportional to the prey's bearing to generate the proportional changes in heading that we observed. The linear relationships between bearing, the change in heading and the tail excursion (Fig. 1C,D) offer perhaps the most rudimentary requirements for a neuromechanical control model of pursuit behavior (Fig. 2ii). A similar form of control may be common to the broad diversity of animals that move by intermittent locomotion and could offer inspiration for the design of robots and autonomous vehicles.

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#### Competing interests

The authors declare no competing or financial interests.

#### Author contributions

Conceptualization: A.P.S., M.J.M.; Methodology: A.P.S., M.J.M.; Software: A.P.S., M.J.M.; Validation: A.P.S.; Formal analysis: A.P.S., M.J.M.; Investigation: A.P.S.; Resources: M.J.M.; Data curation: A.P.S.; Writing - original draft: A.P.S., M.J.M.; Writing - review & editing: A.P.S., M.J.M.; Visualization: A.P.S., M.J.M.; Supervision: M.J.M.; Project administration: M.J.M.; Funding acquisition: A.P.S., M.J.M.

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#### Data availability

Data and code for analysis can be accessed from the Dryad digital repository (Soto and McHenry, 2020): <https://doi.org/10.7280/D1QQ36>

#### Supplementary information

Supplementary information available online at <https://jeb.biologists.org/lookup/doi/10.1242/jeb.230623.supplemental>

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