



Research



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Male dragonflies engage in aggressive aerial contests to establish breeding territories. Using field stereographic recordings of *Trithemis aurora*, we examined dragonfly behavioural objectives during these encounters. Unlike predatory pursuits, in which intercept trajectories minimize time-to-contact, male *T. aurora* steer to keep their opponent in a slightly elevated position within their frontal visual field, modulating speed to avoid direct collision. These contests feature frequent role reversals, with evenly matched rivals alternating between chaser and evader. The manoeuvres observed during these exchanges, including looping and spiralling flight, emerge from the underlying pursuit objectives. During territorial conflicts, males exhibit exceptional agility with centripetal accelerations up to 6g. Despite this high performance, individuals spent approximately one-third of flight time gliding in short bursts, even during close combat. These findings show that complex aerial contests can arise from simple control objectives constrained by sensorimotor limits.

1. Introduction

Pursuit is integral to the flight behaviour of adult dragonflies. A successful male dragonfly must catch small prey items, expel rivals from his territory and intercept females [1–3]. These tasks have a common theme of tracking and chasing another flying insect, but with different behavioural objectives. Classically, pursuits are a contest between two defined roles: that of the pursuer and the evader [4]. This is typically the case in prey and mate pursuits, where the flight patterns or behavioural strategies of chaser and evader differ. Such engagements are asymmetric, with each participant specialized for its role [5]. This is not the case in male–male conspecific engagements. Although males may differ physically [6] or in motivational state, these interactions are contests between similar agents in direct competition. Thus, we expect to see different patterns of behaviour in male–male mutual pursuits [1,7,8].

Combative aerial interactions between equal participants are an important challenge for both animals and aircraft. Close battles between two or more fighter aircraft are called dogfight engagements [9,10], and we have adopted this nomenclature to refer to the interactions between competing male dragonflies otherwise referred to as mutual pursuit [11]. As will be detailed in our results, there are significant similarities between aircraft and dragonfly dogfights, and the use of the term is more than simply aesthetic. Recent work on the automation of combat vehicles forms two distinct streams: (a) decision-based implementation of manoeuvres from a pre-determined library [12,13], reinforcement learning with task-specific reward functions [14], and (b) application of a consistent guidance law to drive steering [15]. Guidance laws are rules that specify how an agent adjust its steering to achieve specific objectives given its current state. Such simple laws can describe the flight trajectories of

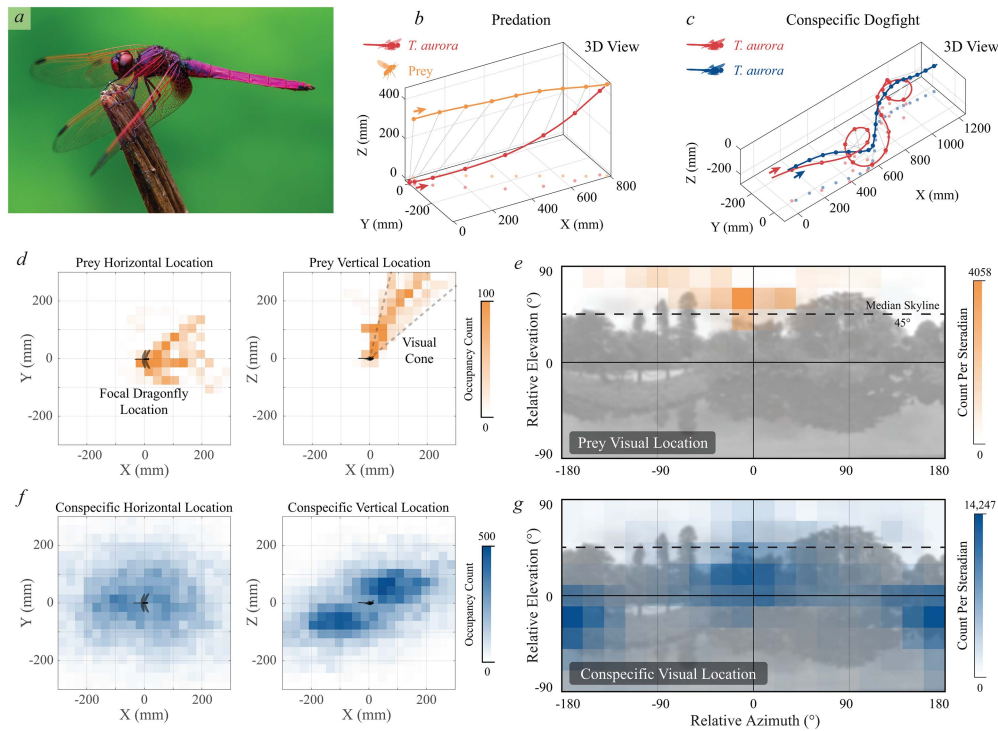


Figure 1. Reconstructed flight trajectories show different flight patterns during the pursuit of prey and conspecifics. (a) A male crimson marsh glider dragonfly (*Trithemis aurora*) in its characteristic pose on a perch in Taipei, Taiwan. (b) Trajectories of prey (orange) interception by *T. aurora* (red) tend to be linear paths towards a future meeting point. LOS between target and dragonfly are drawn at 50 ms intervals. (c) Trajectories of male–male conspecific pursuit do not lead directly to a future meeting point. Males regularly looped around each other without making direct contact. (d) An occupancy histogram shows a vertical cone forward and above the dragonfly in which prey targets are positioned. Illustrated visual cone limits given by the 5th and 95th percentiles of prey elevation. (e) Prey targets as viewed by the dragonfly cluster above the skyline. Prey is thus being viewed against the sky above. A 360° image of the background is underlaid, centred at an arbitrary azimuth. (f) An occupancy histogram demonstrates that conspecific dragonflies form occupancy clusters in front of and behind the dragonfly. (g) Conspecifics in front of the dragonfly are generally at higher altitude, but not enough to clear the skyline of surrounding foliage on average (45° above the horizontal). Thus, conspecifics are generally viewed against a cluttered visual background.

predatory insects [3,16], and raptors [17,18] as they pursue prey. Human visual guidance has also been widely studied using simplified control laws. Proportional navigation and pursuit models have successfully captured human steering and interception dynamics in tasks such as manual target tracking, driving and locomotor interception [19–23]. Time-to-contact-based models also explain human braking and catching behaviour [24,25]. While these phenomenological models cannot resolve the underlying neural implementation of behaviour [26], they offer an algorithmic framework for analysing animal behaviour [27], enabling comparisons across systems through shared control parameters rather than variable movement patterns.

There is a considerable volume of work on the aggressive interactions of many groups of Odonata, with a comprehensive summary in [28]. Earlier studies were restricted to observations by eye, and single camera recording to categorize behaviours of dragonflies engaged in aerial combat, without high-accuracy 3D kinematics [2,29]. To our knowledge, only two previous studies have reported 3D kinematics of dragonfly aerial engagements [1,8], and only one attempted to analyse the steering approach of dragonflies towards conspecifics. The result suggested that dragonflies employ a high-gain proportional control [8], leading to overshooting which was then interpreted as a strategy to ‘herd’ away the competitor. Here, we will go beyond controller characterization and attempt to quantitatively identify the behavioural objectives and determine whether simple guidance laws could account for the observed flight trajectories.

We used a custom stereovideographic, field-portable rig to record aggressive interactions between male *Trithemis aurora* (Burmeister, 1839) dragonflies around the ponds of Taipei Zoo, Taiwan (supplementary material, figure S1). *Trithemis aurora* are crimson-coloured, small (body length 30–35 mm) dragonflies that spend much of their time perched on prominent features around bodies of fresh water (figure 1a). Male *T. aurora* are fiercely territorial and multiple males defend features around a pond. Thus, *T. aurora* makes a superb model species to study the strategies underlying dragonfly aerial dominance contests.

2. Results

This work focuses on capturing conspecific interactions. However, for reference we also reconstructed 9 predatory trajectories in which *T. aurora* intercepted small flying prey (figure 1b). For our main analysis, we used 102 paired trajectories of the dragonfly male–male aerial engagements (figure 1c). These trajectories had a median length of 1.06 seconds (Q1–Q3 = 0.80–1.66 seconds; $n = 204$ trajectories).

2.1. Visual locations of opponents

Trithemis aurora demonstrated this characteristic hunting style of a perching dragonfly (figure 1b; supplementary material, movie S1), approaching prey from below while climbing altitude to catch them from beneath. This contrasted strongly with the highly convoluted trajectories of male–male dogfights (figure 1c; supplementary material, movie S2). Predatory engagements began at close range (median 391 mm; Q1–Q3 = 276–512 mm) and were completed rapidly (median 205 ms; Q1–Q3 = 190–377 ms; $n = 9$ trajectories). The true hunting range of *T. aurora* is likely greater than suggested by these statistics, as we had to reject 18 recordings from analysis as the prey was outside the field of view (FOV) of the cameras. However, these figures are consistent with previous work [3,5].

During interception, dragonflies maintained a characteristic prey tracking cone [30] above and forward of their heading (figure 1d). Prey items had a high elevation relative to the dragonfly at 58° above the horizontal (Q1–Q3 = 52°–66°; $n = 1578$ frames). This was above the median skyline elevation of 45° (Q1–Q3 = 32°–56°; $n = 6080$ vertical slices of 0.06° width around the horizon), suggesting that prey are almost always silhouetted against the sky (figure 1e). The visual position of conspecific opponents during dogfights differed greatly from prey. The median visual elevation of conspecific opponents in the frontal hemisphere was 12.4° (Q1–Q3 = –3.5° to 28°; $n = 30779$ frames). The elevation of pursued conspecific opponents was higher than the median skyline elevation (45°) in only 10.1% of captured frames (3132/30779 frames). To refer to visual positions, we define the line-of-sight (LOS) as the 3D vector between the dragonfly's centre of mass and that of its opponent, equivalent to the range vector. We assume the distance between the dragonfly's centre of mass and retina to have negligible effect on visual input at typical engagement ranges.

During dogfights, conspecifics are either ahead of or behind the focal individual (figure 1f). As a result, any opponents being pursued were often viewed against the ground and surrounding foliage rather than the sky (figure 1g). The symmetric clusters in figure 1f also reflect alternating pursuit states, with dragonflies continuously switching between pursuer and evader roles. For analysis, participants were classified as *at advantage* or *at disadvantage*, following air combat literature terminology [10,13]. We made this classification based on the error angle (angle between velocity vector and LOS) of each participant (figure 2a). During long engagements, dragonflies swapped roles multiple times in tight-turning interactions (figure 2b,c). For 80.1% of our recording time (48 918/61 046 frames), one dragonfly was at advantage (tailing its opponent as a pursuer), while the other was at disadvantage (being tailed) (figure 2d). The rest of the time the opponents were either at mutual disadvantage (both heading towards each other, 10.5% (5168/61 046 frames)), or they were temporarily neutral (both facing away from each other, 9.7% (5902/61 046 frames)).

The visual motion of a target, excluding rotations caused by the dragonfly's own movement, is described by the rotation of the LOS from the dragonfly to the target, here termed the *LOS rate*. The LOS rate varies with the target's velocity relative to the pursuer and is strongly affected by the distance between the target and the pursuer. Opponent conspecific dragonflies tended to be close together, with a median distance of 219 mm (Q1–Q3 = 152–330 mm; $n = 61\,226$ frames). Higher LOS rates present a greater tracking challenge for the dragonfly visual system. For predatory flights the median LOS rate was 124° s^{–1} (Q1–Q3 = 80–265° s^{–1}; $n = 1547$ frames), whereas conspecific flight had a median of 364° s^{–1} (Q1–Q3 = 189–661° s^{–1}; $n = 61\,280$ frames). The mean LOS rate of conspecifics was 2.10 times that of prey (95% CI [1.97–2.22]), Welch's *t*-test on log scale: $t = 24.4$, d.f. = 1652.1, $p < 0.001$ (one-sided).

2.2. The flight performance envelope

Like any flying animal, dragonflies operate within a limited performance envelope of speed and manoeuvrability [31]. Tighter turns at higher speeds require greater lateral accelerations (*g*-loads), creating an inherent trade-off between speed and turning performance [10]. In fixed-wing aircraft, these accelerations must be generated aerodynamically, so low airspeeds reduce control authority and lead to stall, whereas high speeds risk exceeding structural or physiological *g*-limits (supplementary material, figure S2). As flapping fliers, dragonflies can hover and redirect aerodynamic forces largely independent of groundspeed, allowing turning rates to remain high, or even increase, at low speeds, up to spot pirouettes that are impossible for fixed-wing aircraft [10] (supplementary material, movie S3).

During dogfights, *T. aurora* had a median flight speed of 2.1 m s^{–1} (Q1–Q3 = 1.5–2.8 m s^{–1}). This speed range falls far below the top flight speeds from our recordings of *T. aurora* (8.5 m s^{–1}). Dragonflies made high-*g* turns with high frequency during aerial interactions, regularly exceeding 3*g* (figure 2e). Turn radius was strongly limited by flight speed but did not match a consistent maximum centripetal acceleration (*g*-limit) across the flight speed range. To estimate the speed-specific centripetal acceleration limit, we binned centripetal acceleration data by flight speed between 0.5 and 4 m s^{–1} (a range containing 95% of our recorded frames). For each speed bin, we used the 95th percentile of centripetal acceleration as a robust maximum limit. The centripetal acceleration limit rose linearly with flight speed with a gradient of 12.8 s^{–1} ($R^2 = 0.88$; $p < 0.001$) (figure 2f). While increased flight speeds should generate greater flight forces through increased airflow over the wings, dragonflies still turned with a wider radius at high speed (figure 2g).

Unlike many insects, dragonflies glide as well as flap. During aerial engagements, *T. aurora* frequently interspersed flapping with brief glides (figure 2h), with flapping especially common during directional changes (figure 2i). We manually classified frames as flapping, gliding or unclear (3.8% of 53669 frames). Of the determinable frames, 36.8% were gliding and 63.2% flapping, with only slightly higher flapping in advantaged males ($\chi^2(1, N = 51\,323) = 108.8$; $p < 0.001$). Gliding and flapping both occurred in short bouts (median durations 88 and 112 ms, respectively; figure 2j), though glides could last up to 500 ms and flapping up to 1.69 seconds. The wings' operation mode depended strongly on trajectory: gliding was concentrated in near-straight flight, while

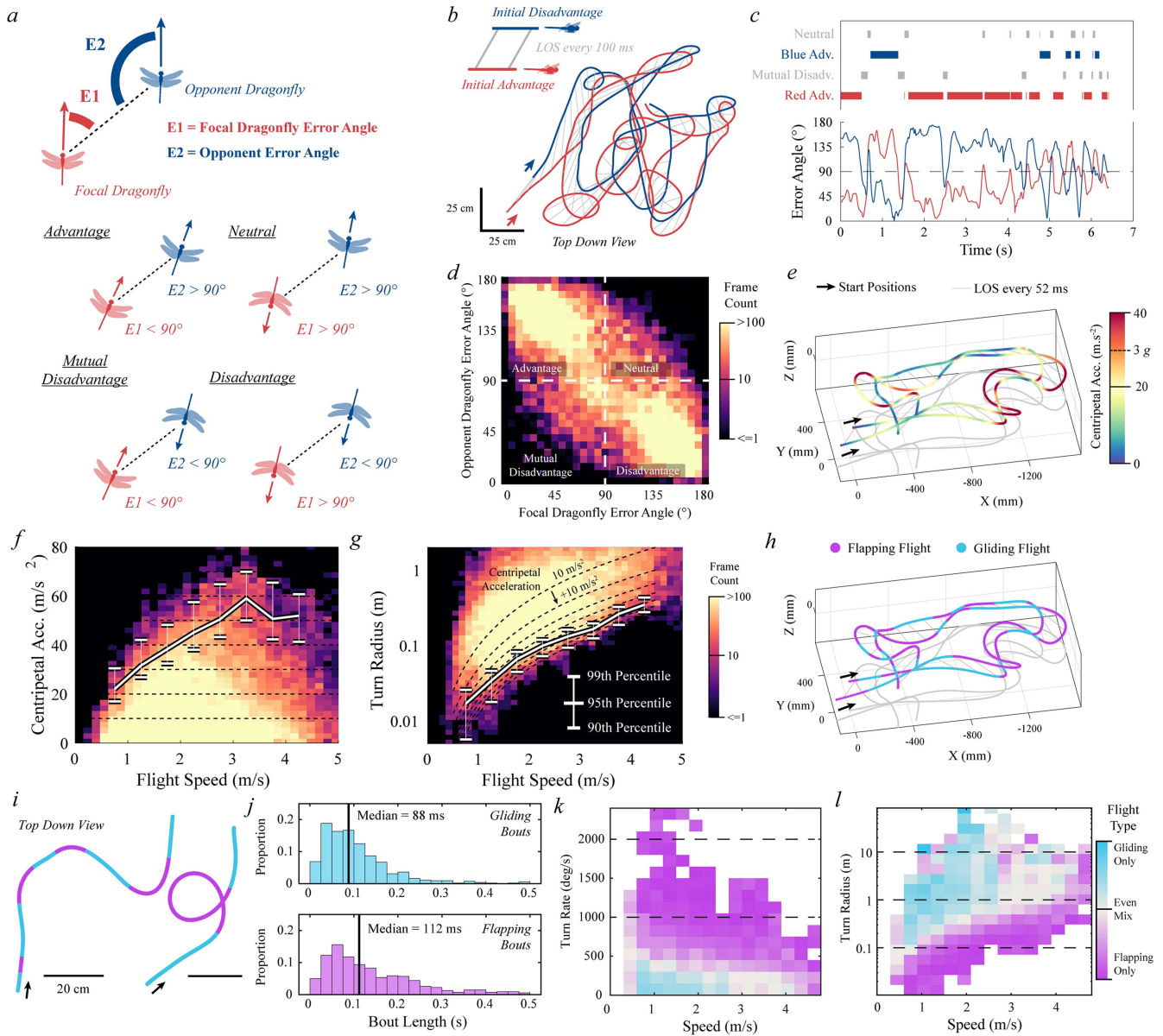


Figure 2. Chase geometry varied greatly as dragonflies demonstrated extreme flight performance capabilities. (a) Dogfights allow for swapping between pursuer–evader identities. We used the geometric condition of a dragonfly and its opponent to describe the relative advantage of each dragonfly. We used the error angles from velocity to the LOS of both participants to define the chase state. (b) A continuous recording of an interacting male dragonfly pair shows the high frequency of turns by both participants. (c) A plot of the error angles of both dragonflies during this interaction (bottom) shows the frequent changes in advantage between the dragonflies (above). (d) An occupancy histogram of dragonfly error angles versus those of their opponents shows the prevalence of asymmetric advantage, which represents a ‘tail chase’ state. (e) An example pair of trajectories from dogfighting dragonflies is coloured by their centripetal accelerations. The frequent sharp turning events of conspecific dogfights regularly exceed $3g$. (f) A histogram shows that higher centripetal accelerations only occurred at higher flight speeds. Bars show the 90th and 99th percentiles of data binned to the nearest 0.5 m s^{-1} . (g) Despite increasing centripetal accelerations, higher speeds increased the dragonflies’ turn radius. (h) The same example pair of flight trajectories as (e) is coloured by the wing state, either flapping or gliding. (i) Example trajectories highlight that flapping was prevalent during turns in the trajectory, with gliding most frequently occurring on straight trajectory sections. (j) Histograms of the length of bouts of gliding (above) and flapping (below). (k) A histogram speed against turn rate is coloured by the prevalence of flapping within each bin. Grey bins have an even mix of both flapping and gliding. (l) The same histogram binning method is applied to turn radius. Large turn radii correspond to more linear sections of trajectory.

flapping spanned the full performance envelope (figure 2*k,l*). In the vertical plane, gliding supported strong downward turns but not other directions (supplementary material, figure S3). *Trithemis aurora* thus function as hybrid flyers, combining flapping manoeuvrability with glide-based efficiency, akin to hybrid unmanned aerial vehicles [32].

2.3. Movements and manoeuvres

2.3.1. Guidance during dogfights

Turning behaviour in dogfighting *T. aurora* was highly correlated to the egocentric position of the opponent. Binning steering responses by opponent azimuth and elevation relative to the dragonfly’s velocity heading (figure 3*a*) showed that lateral opponents

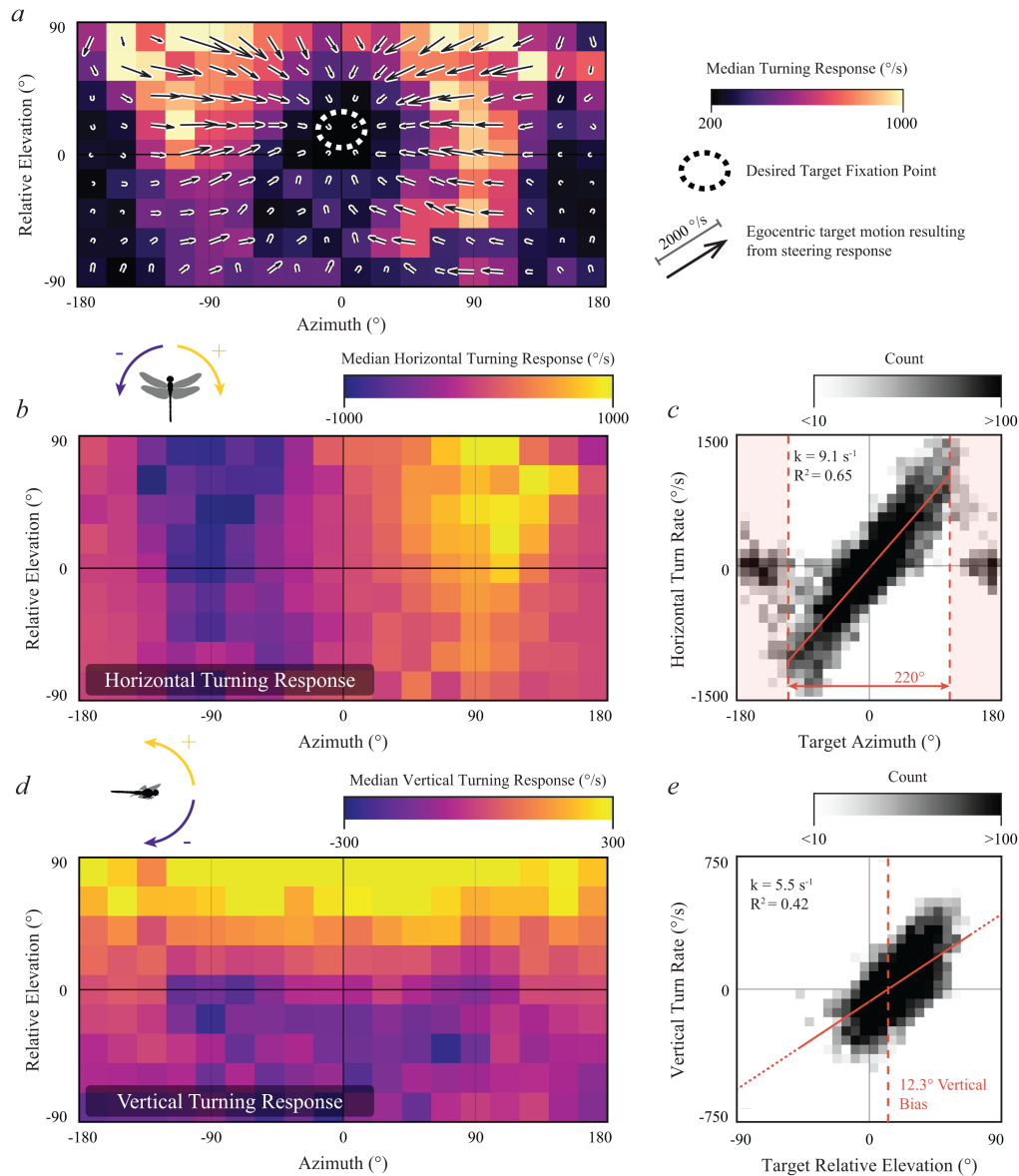


Figure 3. Dragonflies steer to move targets into a forward, slightly elevated visual position. (a) Median turning responses show that dragonflies tend to centre targets marginally above the horizon. Bin shade represents the visual position of the target. Overlaid arrows show the affected egocentric movement of the target position by the dragonfly rotation. (b) Target visual locations generate strong lateral turning responses that do not reach the dragonfly's rear. Bin colour represents the median horizontal turning rate. (c) Dragonfly horizontal turn rate shows a strongly linear relationship to the target's visual azimuth within a forward 220° FOV. (d) A similar map of the target visual elevation and dragonfly turning responses shows a vertical gradient that inflects above the horizon. (e) Dragonfly vertical turn rate shows a strong linear relationship against the target's visual elevation with a non-zero x -intercept, which reflects a 12.3° aiming bias below their targets.

(approx. $\pm 90^\circ$ azimuth) evoked the strongest turning, particularly when located above rather than below the focal dragonfly. Mapping the resulting egocentric motion revealed a strong tendency to steer opponents into a forward, slightly elevated region where turning responses were minimal, which we term the target fixation point. Opponents falling behind elicited inconsistent turning, suggesting either a rear visual blind spot or functionally random 'protean' manoeuvres used to evade a pursuer.

Guidance laws offer a convenient simplified framework to explore the guidance objectives of an autonomous agent. Pure pursuit is expressed by equation (2.1) in which $\dot{\gamma}$ is the pursuer turn rate, ϵ is the error angle between pursuer velocity and the LOS, and k is a gain with units of s^{-1} (supplementary material, figure S4):

$$\dot{\gamma} = k\epsilon. \quad (2.1)$$

The horizontal steering of dragonflies can be captured by this model within the 280° frontal FOV ($\pm 140^\circ$ from pursuer velocity), with a gain k of 7.6 s^{-1} and R^2 of 0.60 ($n = 23438$) (see Methods for model fitting details). Reducing the frontal FOV to 220° ($\pm 110^\circ$) increased the fitted gain (9.1 s^{-1}) with an equivalent coefficient of determination ($R^2 = 0.65$, $n = 21071$), suggesting that the periphery of the FOV included outliers with smaller turn rates than expected by the model (figure 3b,c). The x -intercept of the model (3.7°) was non-significant ($p = 0.12$), demonstrating that steering was symmetrical about the midline. These correlations were obtained under the peak input-output delay of 16 ms (supplementary material, figure S5).

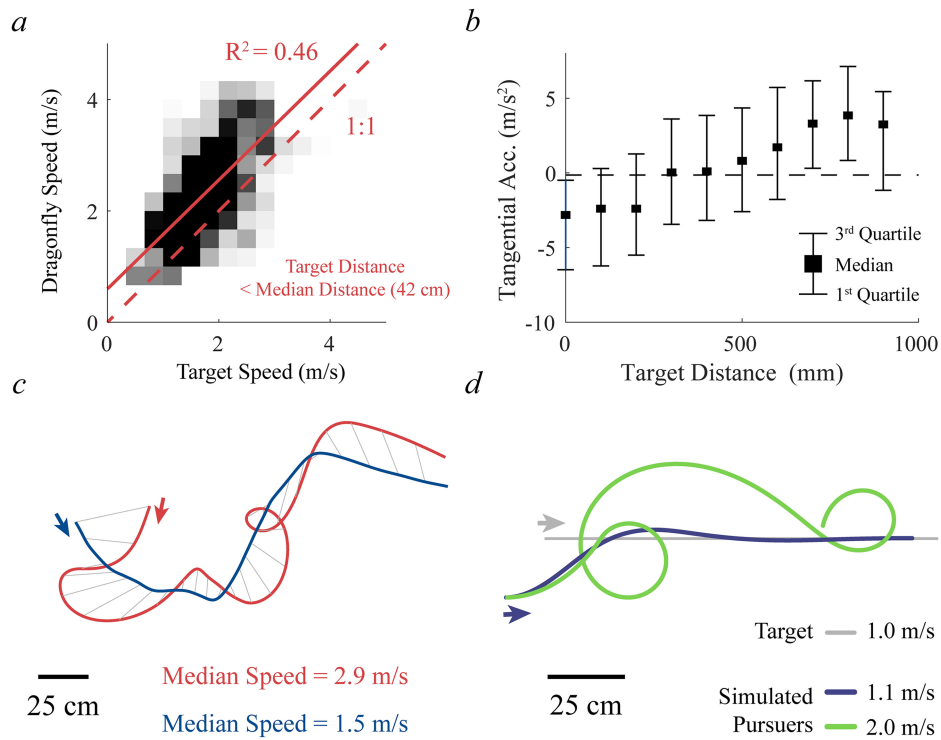


Figure 4. Dragonflies slow and match speeds as they approach artificial targets. (a) Correlation between dragonfly and target speed. Solid line represents a linear best fit, and dotted line shows exact speed parity between dragonfly and target speed. (b) Dragonfly tangential acceleration at different distances relative to target. Negative tangential acceleration represents dragonfly slowing down. Large differences in speed lead to overshooting. (c) In two example trajectories, a dragonfly (red) overshoots or loops the trajectory of its opponent (blue). In these cases, the speed of the overshooting dragonfly greatly exceeds that of its opponent. (d) Two simulated pursuit steering controllers with parameters matched to *T. aurora* fly towards a linearly travelling target, with different fixed speeds (1.1 and 2.0 m s⁻¹). These simulations have no control delay, yet the paths of the high-speed simulation loop and overshoot the trajectory of their target.

To model the dragonfly vertical steering (figure 3d), we restricted our input data to the forward visual field ($\pm 110^\circ$ azimuth) and travelling more than the median flight speed (2.0 m s⁻¹). The model produced a fitted gain ($k = 5.5 \text{ s}^{-1}$) with reasonable goodness of fit ($R^2 = 0.42$; $n = 16\,805$). Notably, the model x-intercept was 12.3° (s.e. 0.21°), matching our earlier observation that dragonflies aim below their rival, rather than directly at them (figure 3a). These correlations were obtained under the peak input–output delay of 28 ms (supplementary material, figure S5).

To estimate sensorimotor delay without assuming a specific control model, we used mutual information between opponent azimuth (binned in 5° left/right) and dragonfly horizontal turn rate (supplementary material, figure S5). This captures how strongly turn rate depends on opponent position without assuming uniform responses across the visual field. Mutual information was highest for lateral opponent positions (above 0.2 bits from 20° to 140°) and low both to the rear ($>140^\circ$) and directly ahead, the latter consistent with steering that drives the opponent towards the forward axis. Calculating mutual information across time lags (-80 to 80 ms, 4 ms steps) revealed a peak of 0.51 bits at a 24 ms delay, consistent with the pure pursuit model and shorter than delays reported for prey interception [26]. Together, these analyses suggest that conspecific chases can be best described by a simple pursuit strategy with low latency in which the dragonfly is trying to keep the opponent fixated directly in front and some 12° above horizon.

2.3.2. Guidance-pursuing artificial targets

To isolate control of speed variation (tangential acceleration), we recorded continuous pursuit trajectories of dragonflies chasing artificial targets moving along circular trajectories (full details in the supplementary material). Dragonflies showed range-dependent speed matching to the artificial target. We divided the speed data at 40 cm, approximately the median target–dragonfly distance, and downsampled measurements to 4 s^{-1} to improve model robustness. At ranges exceeding 40 cm, target and dragonfly speeds were only weakly correlated (slope = 0.28; $R^2 = 0.13$; $n = 7410$). At ranges below 40 cm, dragonflies closely matched target speed (slope = 0.98; $R^2 = 0.46$; $p < 0.001$; $n = 7410$; figure 4a). We then examined changes in dragonfly speed (tangential acceleration) as a function of range. When the target was within 25 cm, dragonflies were typically decelerating (median -2.7 m s^{-2} ; Q1–Q3 = -6.2 to 0.1 m s^{-2} ; Wilcoxon signed rank $z = -33$; $p < 0.001$; $n = 3476$). By contrast, when the target was more than 50 cm away, dragonflies were generally accelerating (median 2.0 m s^{-2} ; Q1–Q3 = -1.6 to 5.5 m s^{-2} ; $z = -25$; $p < 0.001$; $n = 5275$; figure 4b).

It is not clear how dragonflies estimate the distance of their opponent. One plausible cue for distance estimation is target elevation above the horizon. Dragonflies strongly decelerated when target elevation exceeded 15° ($z = -39$; $p < 0.001$; $n = 7574$) but accelerated towards targets closer to the horizontal ($z = 35$; $p < 0.001$; $n = 7492$; supplementary material, figure S6). Because

dragonflies aim beneath their targets, high target elevations occur primarily at close range, making elevation a plausible cue for speed regulation. From our dataset we cannot disambiguate elevation from other potential cues such as angular size or loom rate. Multiple regulatory components may contribute concurrently. Nonetheless, dragonflies tended to reduce speed at close range, which would maintain their tail-chasing role and reduce trajectory overshooting behaviour [8]. Despite this speed control, there were numerous instances in which chasers sustained much greater speeds than evaders leading to overshooting.

2.3.3. Overshooting

During combat, dragonflies often overshoot their opponent's path [8], sometimes leading to a full loop in the horizontal plane (figure 4c). Trajectory overshooting occurs when the pursuer repeatedly crosses the target's path instead of following directly behind. This behaviour was most pronounced when the pursuer was faster than the target (figure 4d). Simulations using a pursuit controller without response delay showed that overshooting and looping can arise purely from high pursuer speed (figure 4d). When speeds are similar, trajectories remain smooth, but higher speeds produce circling and rapid course changes resembling overshooting. In pure pursuit, the controlled variable is the angle between the pursuer's velocity and the LOS to the target. Because the LOS rotates faster at close range, tracking errors arise when the pursuer cannot turn fast enough to match this rotation, even when the target is stationary (supplementary material, figure S7).

This trajectory overshooting differs from the control overshooting described in [8]. Control overshoot occurs when the controlled variable passes its set point owing to excessive gain or response delay [33,34]. By contrast, trajectory overshoot reflects fast LOS changes and arises from insufficient control gains to keep up. Simulations with different damping or delays can produce marginally different trajectories, yet increasing speed creates overshooting (supplementary material, figure S8). Although overshooting might enhance visual display during combat, it also exposes the pursuer to counterattack, allowing the opponent to reverse roles and gain the advantage.

2.3.4. Role reversal

A unique feature of dogfights is the interchangeability of roles. Male dragonfly can be either the chaser or the target. Dragonflies in aerial contests frequently swapped roles using a similar pattern of movement we refer to as changeover manoeuvres (figure 5a; supplementary material, movie S4). Role swaps were generally initiated by the leading dragonfly (starting in disadvantage) performing a laterally downward turn, frequently crossing the path of the trailing dragonfly (starting advantage). He then continued a downward spiral, diving while maintaining the horizontal turn, ending up in the advantaged position. During these manoeuvres, he would generally turn a full loop in the horizontal plane (figure 5b). We excised 31 sections of trajectory in which one of the dragonflies switched from disadvantage to advantage role as defined previously. These excisions had a median length of 432 ms (Q1–Q3 = 376–502 ms). We evaluated these manoeuvres to determine whether they represented a novel mode of control, or whether they could be explained by the same pursuit controller modelled in the previous sections.

We reconstructed the relative visual position of each dragonfly (those starting both with and without a positional advantage) from their opponent's perspective. We then constructed a turn-rate weighting map (figure 5c) using the mean dragonfly turn rate measured across all trajectories (not only changeover manoeuvres). Visual bins (15° in both azimuth and elevation) with turn rates in the top 90th percentile ($>887^\circ \text{ s}^{-1}$) were assigned a weight of 1, and those in the bottom 10th percentile ($<258^\circ \text{ s}^{-1}$) a weight of 0, with intermediate bins scaled accordingly. Multiplying the occupancy of each azimuth-elevation bin by its corresponding turn-rate weight and averaging across bins yielded an *expected turn index* for each sequence of visual positions. Higher values of this index indicate that the opponent occupied visual regions that, on average, elicit strong turning responses in the dragonfly.

To successfully reverse roles, a disadvantaged dragonfly must minimize the time spent within regions of its opponent's visual field that elicit strong responses, while positioning the opponent within high-response regions of its own visual field. As expected, during successful changeover manoeuvres, dragonflies starting with the advantage viewed their opponents in visual regions associated with minimal turning responses (expected turn index = 0.09; $n = 3337$ frames) (figure 5d). By contrast, initially disadvantaged dragonflies showed the opposite pattern (figure 5e), with a maximum index score of 0.53 ($n = 3337$ frames). Plotting a representative visual trajectory from the initial pursuer's perspective reveals that the manoeuvre involves a downward and lateral movement, steering away from high-response regions (figure 5d,e).

In some of reconstructed interactions ($n = 7$), the changeover was not successful as the initial chaser followed the initial evader into the initial downward loop (figure 5f). These interactions resulted in a descending spiral with both dragonflies orbiting one another (figure 5g; supplementary material, movie S5). This spiral was notably different from the 'spiral threat' described in [29], as the dragonflies were both laterally positioned to each other and travelling at speed, rather than face to face at close range. Both dragonflies completed multiple full loops in the horizontal plane, and we observed a maximum of four full orbits for a single encounter. Eventually, one participant would break from the spiral and flee, assuming a disadvantage position. During spiralling manoeuvres (figure 5f,g), the relative target location was mirrored between each male (figure 5h,i), with both spending time in each other's high-response regions. Both starting advantage and starting disadvantage had high expected turn indexes of 0.48 and 0.67, respectively ($n = 1256$ frames each). This symmetry between participant visual cues plausibly suggests descending spirals are the consequence of both dragonflies operating the same visual steering strategy in a roughly symmetric geometry.

To further explore the dynamics of a changeover manoeuvre, we fitted linear models to the horizontal turn rate of both dragonflies (starting advantage and disadvantage) in response to their opponent's azimuthal position during changeover manoeuvres, as we had done for the entire dataset (supplementary material, figure S9). The fitted model for starting advantage dragonflies was a

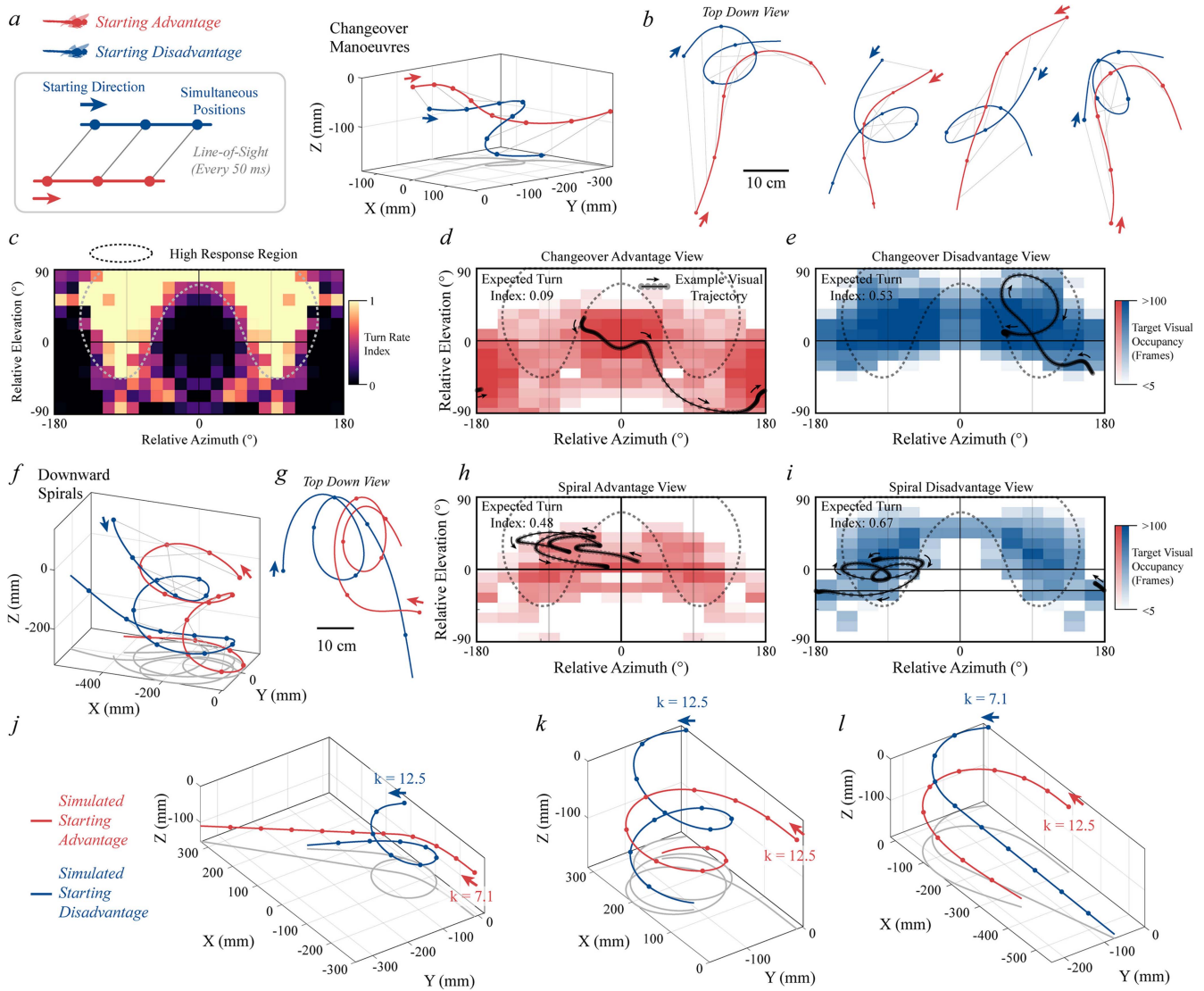


Figure 5. Repeated duelling patterns are consistent with the male dragonfly visual steering strategy. (a) Example changeover manoeuvre trajectories of dragonflies starting at a disadvantaged position (blue) swapping roles with their pursuer (starting advantage, red). (b) Further example changeover manoeuvres show the repeated motif of a full turn in the horizontal plane, when viewed from top-down. (c) Reference map of expected turning for a given target visual location. The dashed boundary illustrates a visual high-response region in which targets stimulated strong turning reactions. This map, normalized between 0 and 1, is used to create the expected turn index, where 1 represents maximal expected turning for a given target angular location. (d) The visual position of opponents is mapped across an occupancy histogram from the perspective of the dragonfly starting in advantage during excised changeover manoeuvres. Dashed boundary shows the high-response visual region. Solid line and scattered points show an example visual trajectory. (e) A visual occupancy histogram from the perspective of the dragonfly starting in disadvantage. The example visual trajectory is the dyad pair of that given in (d). (f) Dogfighting dragonflies also entered mutual descending spirals. (g) A top-down view of a second example spiral demonstrates that during these interactions, both dragonflies complete multiple full loops in the horizontal plane, until one of them breaks from the engagement. (h) An occupancy histogram of the visual position of the opponent dragonfly from the perspective of the dragonfly starting in advantage, during excised downward spiral manoeuvres. Solid line and scattered points show an example visual trajectory. (i) An occupancy histogram of the visual position of the opponent dragonfly from the perspective of the starting disadvantage, during excised downward spiral manoeuvres. The example visual trajectory is the dyad pair of that given in (h). Simulations of agents using the fitted steering controllers produce changeovers (j), spirals (k) or simple turns (l) depending on pursuit gain k . Changeovers occur when disadvantaged agents have higher gains than advantaged agents; spirals when gains are matched; and simple turns when advantaged agents have higher gains. High and low gain values (7.1 and 12.5 s^{-1}) were taken from fits to excised manoeuvre trajectories.

close match to that of the entire dataset ($k = 7.1$ s^{-1} ; $R^2 = 0.57$; $n = 1832$; $p < 0.001$), while the model fitted for starting disadvantage dragonflies had a higher gain ($k = 12.5$ s^{-1} ; $R^2 = 0.81$; $n = 1963$; $p < 0.001$). During spiral manoeuvres, the fitted models for both dragonflies starting in advantage ($k = 14.7$ s^{-1} ; $R^2 = 0.75$; $n = 929$; $p < 0.001$) and starting in disadvantage ($k = 11.0$ s^{-1} ; $R^2 = 0.77$; $n = 748$; $p < 0.001$) had high gains, compared with the entire dataset ($k = 8.8$ s^{-1}).

We applied the control gains measured from our excised changeover and spiral manoeuvres to simulated agents (see Methods for details). In each simulation, we kept the same starting conditions of one agent in disadvantage, with the other in advantage behind at a distance of 30 cm. Both agents started with matched fixed speed. When the agent starting in disadvantage was given the higher gain ($k = 12.5$ s^{-1}) and the agent in advantage the lower gain (7.1 s^{-1}), the outcome of the interaction replicated a

changeover manoeuvre (figure 5j). However, if both agents were initiated with identical high gains (both $k = 12.5 \text{ s}^{-1}$), then the resulting trajectories resembled downward spiral manoeuvres (figure 5k). As a further test, we reversed the changeover manoeuvre gains and gave the agent starting in advantage the higher gain ($k = 12.5 \text{ s}^{-1}$) and the agent starting in disadvantage the lower gain (7.1 s^{-1}). Under these conditions, the agent starting in advantage was able to follow the turn and retain its advantaged position (figure 5l). The manoeuvre resembled an unsuccessful evasive turn by the agent starting in disadvantage.

3. Discussion

Dragonfly dogfights alternate between phases of steady linear flight and sudden, tight-turning engagements, reflecting transitions between slowly and rapidly changing pursuit geometries. Males steer strongly towards opponents located laterally, weakly towards those directly ahead, and show little consistent steering towards opponents behind them. The aerial combat strategy of dragonflies can be well captured by a pure pursuit guidance law, with a vertical deviation. However, this does not necessarily imply that dragonflies employ a continuous feedback system in which the opponent's visual position directly drives turn rate. The pure pursuit guidance law describes the overall steering strategy, but there are multiple routes to the detailed behavioural implementation. Dragonflies could make many discrete turning decisions based on multiple pathways of visual information and internal models [26], that when combined, resemble a simpler linear control strategy.

Our pure pursuit model of the interactions of *T. aurora* differs from previous work in another species [8]. Namely, we do not find evidence of virtual-point, interceptive pursuit [15], nor do we find that dragonfly pursuit is under-damped for the measured control delays (approx. 20 ms), as found by Lohman *et al.* [8]. Male *T. aurora* generally matched the speed of their opponent, but there are clear exceptions when pursuers travel much faster than their opponents. Pursuers with substantially higher speeds than their opponents did not exploit this advantage to achieve collision or capture. Instead, looping and overshooting are inherent to the pursuit controller (even without delay), especially when the pursuer is faster than its opponent. We agree with Lohman *et al.* [8], however, that this feature could serve the display function of pursuit flights, showcasing a male's bright dorsal colouration [2,7].

While we have framed our results in the context of dragonflies, Anisoptera (the dragonfly suborder of Odonata) are a diverse group with different flight behaviours. In our recordings, male *T. aurora* never directly contacted each other. This is in strong contrast to other dragonfly species in which male–male contact and even biting form a component of intra-sexual conflict [29,35,36]. Unlike other species of Odonata [2,29], we did not observe a 'threat' behaviour that was distinct from pursuit, such as face-to-face wing fluttering or rocking. Thus, non-contact pursuits appear to be the primary means of intra-sexual conflict in *T. aurora*. What remains unclear is how victory is achieved. In a dogfight between fighter jets, maintaining the advantage position long enough enables weapon deployment. In the dragonflies' aerial contests, obtaining an equivalent advantageous position is evidently the goal, as indicated by their pursuit behaviour. Beyond potentially lying in an opponent's visual blind spot, it remains uncertain why this position confers an advantage beyond symbolic dominance.

The study highlights the distinct visual demands of prey interception versus conspecific combat. Fighting males typically view one another against a visually cluttered background instead of the clear sky (as in predation), suggesting that the neural circuits for target detection may differ from those used in prey capture. Furthermore, the lateral viewing angle also highlights body colouration [7], merging pursuit and display into a single show of fitness. Yet why would another male take notice if such displays rarely have consequences? One possibility is that contact, though infrequent, is extremely costly. Studies of non-contact pursuits in Odonata have occasionally observed collisions [37], which frequently resulted in death of one of the participants [2,36]. In our dataset, the mutual downward spirals (figure 5f) frequently brought contestants close to the water surface. Had one dragonfly failed to pull out of the spiral, the leading dragonfly or both could have crashed. This extreme, occasional penalty may be sufficient to maintain implied threat during pursuit conflicts.

A limitation of our study is that we could not track individual identities across recordings, so our analysis conflates both inter- and intra-individual variation. Our model uses a single gain to convert opponent angular position into turn rate, limited by the maximum turn rate achievable at a given flight speed. During changeovers, dragonflies gaining advantage showed higher gain than those losing it, suggesting elevated aerodynamic force production and/or motivation. Here, we use 'motivation' to mean a willingness to operate near maximal turning, which cannot be measured directly but suspected to differ between residents and intruders [35]. Territorial residents are typically more motivated to defend than intruders are to invade, producing the resident-favouring bias seen in Odonata and other insects [38–41]. In tight spirals, both males showed high gains, and these interactions often occurred between males with nearby territories, consistent with mutually high motivation and the strong escalation reported when resident–intruder roles are ambiguous [42]. Future kinematic studies should track individuals and distinguish residents from intruders to test for systematic behavioural differences.

It is surprising that even during intense aerial combat, dragonflies are gliding for near one-third of the time. This may indicate that either energetic conservation or thermal limits are an important consideration during extended interactions. It is also possible that gliding creates a more stable visual condition in which to track the target. We only observed gliding during sections of flight with little curvature. This indicates that strong turning requires additional control inputs only available through flapping. We defined flapping by any wing movements and could not distinguish the effort dragonflies apply. Dragonflies use a direct linkage between their flight muscles and wing bases, which enables a fully independent and dynamic control output than the indirect flight system found in other insect groups [43]. Thus, wing movement may be used to trim the balance during gliding flight, rather than providing the thrust for lift or forward acceleration [1].

Dragonfly aerial combat closely resembles that of human fighter pilots, with opponents competing to gain an advantaged, tail-chasing position. The convergence is likely driven by similar sensory constraint, with fighter jets' forward-facing weapon-radar systems and dragonflies' frontally biased vision both favouring target detection ahead. Human pilots in combat scenarios tend to use pure pursuit [44], adjusting lag or lead angles to respectively increase or decrease range. Aircraft dogfights also feature high-g manoeuvres, in which pilots will aim to maintain the optimal airspeed for higher turn rate, rather than simply achieving maximum speed. These contests may include downward vertical turns and spirals [10] that strongly resemble the manoeuvres of dragonflies. A point of contrast between aircraft and dragonfly dogfighting strategies is the use of potential energy. Fighter pilots treat altitude as a reserve of potential energy that can be traded for airspeed during combat through diving manoeuvres [10]. For an equivalent speed, the pilot would rather be higher in altitude than their opponent. Dragonflies do not appear to use altitude in this way, instead preferring to position themselves slightly below the opponent, without an energy advantage but with a potential visual tracking advantage.

In summary, male *T. aurora* exhibit an aerial combat strategy that is well described by a pursuit guidance law. Their behavioural objective appears to be simply keeping the opponent in their frontal visual field. Success in such contests demands rapid reactions and tightly coordinated, high-gain control, demonstrating aerial skill while avoiding collision. The resemblance between dragonfly and human aerial combat underscores the emergence of convergent pursuit strategies under similar objectives. Future work integrating individual identification and high-resolution kinematic tracking will clarify how visual tracking (e.g. gaze tracking), behavioural state (e.g. contest history) and environmental conditions (e.g. territorial boundaries) interact to shape these remarkable competitive interactions.

4. Methods

4.1. Flight trajectory recordings

We recorded *T. aurora* using a field-portable stereovideographic rig (supplementary material, figure S1). We used two shutter-synchronized Chronos 2.1 (Kron Technologies) cameras to record interactions (one colour, one monochrome). We used a cross-arm (Calumet) to maintain a 70 cm separation between the cameras. We used Nikkor 24 mm F 2.8 lenses to ensure each camera had a wide FOV with minimal distortion. This configuration resulted in a resolution of 0.02° per pixel across a 40° FOV. While exact coverage varied between different camera orientations, we generally aimed to cover an area $2 \times 2 \times 1.5 \text{ m}^3$ (width $\times$ depth $\times$ height). Aerial contests were generally limited to the area above the water's surface; thus, the far bank of the pond frequently represented our depth limit, around 4 m from the camera rig.

We recorded videos at 250 fps, a frame rate chosen to provide sufficient temporal resolution to capture rapid flight manoeuvres while preserving a relatively long buffer in memory. We used a manual trigger to record 2000 frame videos of interactions (8 seconds real time at 250 fps). This approach allowed us to capture extended chase sequences while keeping file sizes manageable and limiting the number of interactions per video.

4.2. Camera rig calibration

We moved a known-sized checkerboard (4 cm^2 , 7×8 squares) forward and back in front of both cameras, aiming to cover as much depth and FOV as possible. We used the MATLAB (2022b MathWorks) Stereo Camera Calibrator application to detect the square corners of the checkerboard. This application also estimated both the camera intrinsics (focal length, optical centre, and distortion) and camera extrinsics (relative camera translation and rotation).

To define true global horizontal, we digitized ≥ 5 points on the pond surface in DLTdv8 [45] and triangulated them using the checkerboard calibration. We then performed principle component analysis on these 3D points to estimate the water plane (first and second principal components) and took its normal vector as the gravity-aligned vertical axis. All flight reconstructions were rotated so this plane matched the global X–Y plane, with the Z-axis pointing vertically upward.

4.3. Digitization of trajectories

We created a custom-written MATLAB (2022b MathWorks) application similar to that in [46] to track interacting dragonflies and their targets (supplementary material, figure S1). Full details of how our tracking application works are given in the supplementary material. Our median reprojection error of digitized dragonfly locations was 1.2 pixels ($N = 204$ trajectories; $n = 63\,031$ reconstructed positions; Q1–Q3 = 0.5–2.3 pixels).

4.4. Reconstruction of trajectory kinematics

Coordinate estimates from stereo photogrammetry contain spatial noise, especially in depth, so trajectories were filtered before deriving kinematics (supplementary material, figure S1). We removed raw position estimates with high reprojection error (>5 pixels) or large deviations from predicted position ($>30 \text{ mm}$, approx. body length), then fitted cubic smoothing splines using csaps (Curve Fitting Toolbox, MATLAB). This approach suits the curved, non-stop flight of dragonflies. The smoothing parameter $p = 0.003$ penalized trajectory roughness while preserving curved paths, yielding realistic second-order kinematics and did not

cut corners. The final splines closely matched the raw data (median raw-smoothed displacement 5.8 mm; Q1–Q3 = 3.0–11.5 mm; $N = 204$ trajectories; $n = 63\,031$ positions).

Centripetal acceleration was computed as speed (m s^{-1}) $\times$ turn rate (rad s^{-1}) and converted to g by dividing by 9.8 m s^{-2} .

4.5. Models and statistics

All model fitting and statistical analysis were performed in MATLAB (2022b MathWorks). Throughout our reporting we favour medians with the first and third quartiles (Q1–Q3) as our data were rarely normally distributed. To perform χ^2 tests, we used the MATLAB inbuilt function *crossstab*. To perform Welch's t -test, we used the inbuilt MATLAB function *ttest2* with the variance type set to 'unequal'.

To produce linear fits of our pursuit guidance models, we fitted a robust linear regression using iteratively reweighted least squares with Tukey's bisquare loss (*fitlm* in MATLAB R2022b; default tuning). At high elevations, the angular separation between different azimuthal bearings is reduced (near the pole, a small shift in position can change the azimuth by 180°). For this reason, we discarded azimuth data at elevations more than 70° . The x -intercept of the elevation model was computed as $-\beta_0/\beta_1$, where β_0 is the fitted y -intercept and β_1 is the fitted gradient. The x -intercept standard was obtained using Fieller's method based on the robust coefficient covariance matrix. Mutual information between opponent azimuth and dragonfly turning response was estimated using the k -nearest neighbour method of Kraskov *et al.* [47], given by

$$I(X; Y) = \psi(k) + \psi(N) - \frac{1}{N} \sum_{i=1}^N \left[\psi(n_x(i) + 1) + \psi(n_y(i) + 1) \right], \quad (4.1)$$

where $\psi(\cdot)$ is the digamma function, N is the number of samples, k is the number of nearest neighbours, and $n_x(i)$, $n_y(i)$ are the number of neighbours within the k th nearest neighbour distance in the marginal spaces.

4.6. Simulations

We simulated the dragonfly guidance system in MATLAB (2022b Mathworks) with 1 ms time steps over 500 ms. Each pursuer agent was defined by position and velocity, moved at a fixed speed of 1.5 m s^{-1} , and tracked its opponent as the target. At each step, the LOS vector to the target was computed, and its azimuth and elevation relative to the pursuer's velocity set horizontal and vertical steering via a proportional controller with gain k , applied to LOS angles delayed by 20 ms to match measured sensorimotor delay. Pursuers had a finite visual field ($\pm 120^\circ$ azimuth); when the target lay outside this range, steering was zero. Vertical steering included a 15° elevation bias to maintain aim below the target. Velocity vectors were updated by sequential yaw and pitch rotations (axis–angle), keeping speed constant. Simulations stopped at the maximum run time, and the MATLAB code is provided in the supporting material.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Data and code associated with our work are accessible via Dryad [48]. Our supporting data include all recorded trajectories of male *T. aurora* in aerial combat along with the handling scripts required to replicate our results and figures. There is also a readme file that describes the contents of each .mat file. Additionally, we have provided scripts for our agent-based simulations of the pure pursuit guidance law.

Supplementary material is available online [49].

Declaration of AI use. We used ChatGPT (Open AI, GPT-5, 2025) to assist in improving the clarity, concision and grammatical quality of the manuscript text. The tool was employed under the direct supervision of the authors and did not contribute to the conception, analysis, interpretation or conclusions of our study.

Authors' contributions. S.T.F.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; A.M.Y.: formal analysis, investigation, writing—review and editing; S-L.C.: conceptualization, funding acquisition, project administration, resources; H-T.L.: conceptualization, funding acquisition, investigation, project administration, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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