SYMPOSIUM

Capture Success and Efficiency of Dragonflies Pursuing Different Types of Prey

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Synopsis The dynamics of predator–prey interactions vary enormously, due both to the heterogeneity of natural environments and to wide variability in the sensorimotor systems of predator and prey. In addition, most predators pursue a range of different types of prey, and most organisms are preyed upon by a variety of predators. We do not yet know whether predators employ a general kinematic and behavioral strategy, or whether they tailor their pursuits to each type of prey; nor do we know how widely prey differ in their survival strategies and sensorimotor capabilities. To gain insight into these questions, we compared aerial predation in 4 species of libelluid dragonflies pursuing 4 types of dipteran prey, spanning a range of sizes. We quantified the proportion of predation attempts that were successful (capture success), as well as the total time spent and the distance flown in pursuit of prey (capture efficiency). Our results show that dragonfly prey-capture success and efficiency both decrease with increasing size of prey, and that average prey velocity generally increases with size. However, it is not clear that the greater distances and times required for capturing larger prey are due solely to the flight performance (e.g., speed or evasiveness) of the prey, as predicted. Dragonflies initiated pursuits of large prey when they were located farther away, on average, as compared to small prey, and the total distance flown in pursuit was correlated with initial distance to the prey. The greater initial distances observed during pursuits of larger prey may arise from constraints on dragonflies' visual perception; dragonflies typically pursued prey subtending a visual angle of 1°, and rarely pursued prey at visual angles greater than 3°. Thus, dragonflies may be unable to perceive large prey flying very close to their perch (subtending a visual angle greater than 3–4°) as a distinct target. In comparing the performance of different dragonfly species that co-occur in the same habitat, we found significant differences that are not explained by body size, suggesting that some dragonflies may be specialized for pursuing particular types of prey. Our results underscore the importance of performing comparative studies of predator–prey interactions with freely behaving subjects in natural settings, to provide insight into how the behavior of both participants influences the dynamics of the interaction. In addition, it is clear that gaining a full understanding of predator–prey interactions requires detailed knowledge not only of locomotory mechanics and behavior, but also of the sensory capabilities and constraints of both predator and prey.

Introduction

The dynamics of predator–prey interactions vary enormously, depending on the substrate or medium in which they occur, and on the motor and sensory systems of predator and prey. Encounters can range from active chases, in which prey attempt to actively evade pursuing predators, to ambush predation, in which predators pounce on unsuspecting prey. To further complicate matters, most predators pursue a range of different types of prey, and most organisms are preyed upon by a variety of predators.

Because mechanistic studies of predatory interactions are scarce, we do not yet know whether predators employ a general kinematic and behavioral strategy when pursuing different prey, or whether

they tailor their pursuit to each type of prey; nor do we know how widely types of prey differ in their survival strategies and sensorimotor capabilities. Many previous studies concerning sensory and/or mechanical aspects of predation and escape have focused on the rapid predatory strikes (Maldonado et al. 1967; Tanaka and Hisada 1979; Rand and Lauder 1981; Webb and Skadsen 1980; Vincent et al. 2005; Higham 2007) or startle–escape responses (e.g., Webb 1976; Yager et al. 1990; Domenici and Blake 1997) involved in ambush predation, or occasionally the mechanics of both behaviors in the same organism (Harper and Blake 1991; Schreifer and Hale 2004). These behaviors occur over relatively short spatial and temporal scales, and thus can be studied more easily than prolonged, active chases that cover large areas. In many cases, artificial stimuli or simulated predators are used to evoke escape responses (e.g., Srygley and Kingsolver 2000; Meager et al. 2006; Almbro and Kullberg 2008), and tethered prey are used to elicit predatory searches or strikes (e.g., Ghose and Moss 2003; Chiu et al. 2010).

In addition to the scarcity of detailed mechanistic studies of natural predator–prey interactions, very few studies have compared the performance of predators pursuing different types of prey, or of prey being pursued by a variety of predators (but see Juanes and Conover 1994; Webb 1984, 1986), although this situation is nearly ubiquitous in nature. In addition to providing insight into natural communities, determining how alternative predator–prey combinations differ from one another will help reveal how general predator–prey interactions are, and how much we can extrapolate from mechanistic studies of a single predator–prey pair.

Dragonflies are well known for their aerial predatory abilities (with up to 97% capture success; Olberg et al. 2000) and for their opportunistic pursuit of a wide variety of flying prey (Baird and May 1997). Predatory behavior and performance have been studied in the wild for a few species of "perching" dragonflies, which stake out spots of high prey density and leave their perches only to pursue prey flying overhead or to engage in territorial behaviors (Baird and May 1997; May and Baird 2002). The visual neurobiology and interception strategies underlying dragonfly aerial predation have been studied extensively (Frye and Olberg 1995; Labhart and Nilsson 1995; Olberg et al. 2000, 2005, 2007; Gonzalez-Bellido et al. 2013), but the flight mechanics of predator and prey have received less attention (Combes et al. 2012).

Performance during predation is critical for dragonflies, as the gain in mass associated with predation directly affects the fitness of both males and females—in females by increasing fecundity (Anholt 1991), and in males by increasing the ratio of flight muscles to total body mass, which enhances acquisition of territories and improves mating success (Marden 1989). However, individuals who spend more time foraging also suffer increased mortality due to the risk of being attacked while hunting (Anholt 1991), and territorial species risk losing their spot to competitors while they are occupied with the pursuit and handling of prey (Baird and May 2003).

Thus, some aspects of predatory performance in dragonflies (proportion of successful pursuits, time away from the perch, and distance traveled per attempt) may have consequences not only in terms of energetics (gains associated with successful captures, costs of failed attempts or longer chases), but also in terms of risk of mortality and potential loss of valuable feeding or mating territories. A dragonfly can increase its energetic intake by improving its proportion of successful pursuits and/or increasing the size of prey consumed. Energetic costs can be reduced by minimizing the distance traveled and time spent capturing prey, which may also lower the risk of mortality and loss of territory.

In this study, we addressed the question of how general predator–prey interactions are by comparing the performance of four species of libelluid dragonflies pursuing four different types of prey in an enclosed, outdoor habitat. We performed controlled predation trials to quantify the proportion of pursuits that are successful (hereafter "capture success"), and filmed successful pursuits with high-speed video to determine the total time spent and distance traveled to capture the prey (as approximations of a dragonfly's "capture efficiency," which is not necessarily equivalent to energetic efficiency). The dragonflies tested all co-occur in the same foraging habitat and represent several different size classes, with one small, one intermediate, and two larger species. The prey used in feeding trials spanned a wide range of sizes, and included fruit flies, mosquitoes, houseflies, and deerflies.

We used the data from these experiments to address two main questions. First, how does the size of prey affect the capture success and efficiency of hunting dragonflies? Because larger insects generally fly faster than smaller ones, we expected that larger prey would be more difficult for dragonflies to catch, resulting in longer pursuits that took dragonflies further from their perch (reduced capture efficiency), and in more failed predation attempts (reduced capture success).

Second, we asked how the identity and relative size of dragonflies affect their performance during

predation. If dragonfly–prey encounters are primarily driven by the flight mechanics and behavior of the prey (as has been shown in some cases) (Combes et al. 2012), we might expect that the four dragonfly species tested would display similar success and efficiency when pursuing each type of prey. Alternatively, if dragonflies' flight speed plays a key role in predator–prey interactions, we might find that the scaling of flight speed with body size results in a clear relationship between the relative size of dragonflies and their performance during aerial predation. However, if other features of flight performance (e.g., acceleration, maneuverability) or predatory behavior are more important, we may find that certain dragonfly species are particularly well suited to capturing particular types of prey, and thus that the identity of dragonflies is more critical than their relative size in determining predatory performance.

Materials and methods

Predation trials and measurement of capture success

Dragonflies were captured at a pond in Bedford, MA June–September 2012 and released into a large greenhouse (7.3 × 7.3 × 4.6 m high). The greenhouse contains shrubbery and artificial ponds, and is enclosed by wide-mesh screening that allows small prey, as well as natural light and air currents to enter the habitat (see Combes et al. 2012). Dragonflies were allowed to acclimate to the greenhouse for at least 1 day, and most individuals rapidly began perching and feeding on aerial prey. Four species of perching dragonflies from the family Libellulidae were used for predation trials (Fig. 1A–D): *Sympetrum rubicundulum* (the Ruby Meadowhawk), *Pachydiplax longipennis* (the Blue Dasher), *Libellula cyanea* (the Spangled Skimmer), and *Libellula semifasciata* (the Painted Skimmer). These four species span a range of sizes, from the small Ruby Meadowhawk (∼33–35 mm) to the intermediate Blue Dasher (∼35–43 mm), to the larger skimmers (∼40–48 mm). Both males and females were used for predation studies; no obvious differences in performance were noted qualitatively, and we assessed the effect of sex on measured variables using a *t*-test or a Kruskall–Wallis test in SPSS (depending on sample size) for species with sufficient trials on both males and females.

During feeding trials, we released prey near perched dragonflies (approximately level with the dragonfly and ∼15–30 cm away) by opening the top of a chamber containing one type of prey, and allowing individuals to emerge spontaneously. In
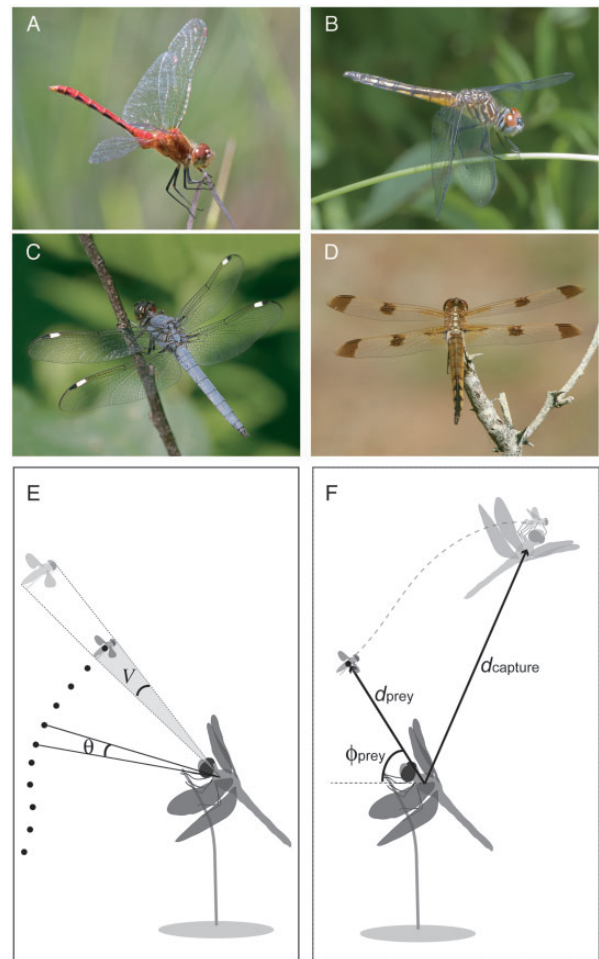

Fig. 1 Dragonflies used in predation trials and variables measured from high speed videos. (**A**) Ruby Meadowhawk (*Sympetrum rubicundulum*) male. (**B**) Blue Dasher (*Pachydiplax longipennis*) female. (**C**) Spangled Skimmer (*Libellula cyanea*) male. (**D**) Painted Skimmer (*Libellula semifasciata*) male. (Images in A–D copyrighted and printed with permission of Glenn Corbiere.) (**E**) Variables measured concerning motion of the prey prior to dragonfly take-off. Prey position was digitized in the 10 frames prior to take-off (black dots) and used to calculate translational velocity and angular velocity of the prey relative to the dragonfly ($\Delta\theta$/time), as well as the visual angle subtended by the prey (V); light gray image demonstrates how larger prey located farther from the dragonfly subtend the same visual angle as smaller, closer prey. Calculated variables were averaged over the 10 frames (102 ms) prior to take-off. (**F**) Variables measured concerning prey capture include the initial distance of the prey from the dragonfly at the time of take-off (d_{prey}), elevation angle of the prey at take-off (ϕ_{prey}), total time to capture, and linear distance to the site of capture ($d_{capture}$).

cases when the dragonfly pursued the prey, we scored the chase as successful if mastication was observed after the dragonfly returned to its perch. We conducted 480 trials with four different types of dipteran prey: fruit flies (*Drosophila melanogaster*, reared in the laboratory), mosquitoes (captured wild,

containing a mix of diurnal species including *Aedes vexans*), houseflies (*Musca domestica*, reared in the laboratory), and deerflies (*Chrysops* sp., captured wild). The prey spanned a range of sizes, from small fruit flies (~2–3 mm) to intermediate mosquitoes (~2.5–7 mm), to larger houseflies (6–7 mm) and deerflies (7–10 mm). Not all prey types were available to be tested on each of the four dragonfly species, and not all dragonflies would pursue all prey types; houseflies were tested on *S. rubicundulum* and *P. longipennis*, deerflies on *L. cyanea* and *L. semifasciata*, and fruit flies and mosquitoes on all four dragonfly species.

Average capture success for each dragonfly-prey combination was calculated as the number of successful captures divided by the total number of pursuits, with all trials of a given dragonfly–prey combination pooled together. We were not able to collect sufficient trials from individual dragonflies pursuing each prey type to determine whether an individual's capture success varies for each combination, but we have previously shown that individual variability in capture success is insignificant for one of these dragonfly–prey combinations (*L. cyanea* pursuing fruit flies; Combes et al. 2012). Binomial proportion confidence intervals for capture success measurements were calculated at 95% in SPSS using the Wilson score interval, which performs better than the normal approximation interval for small sample sizes and extreme proportions (Wilson 1927). Average capture success of the four dragonfly species pursuing fruit flies versus mosquitoes was compared using a paired *t*-test in SPSS.

High-speed filming and measurement of capture efficiency

We recorded approximately 200 predation trials with high-speed video, using multiple synced video cameras (Photonfocus MV1-D1312-160-CL-12, 8-camera system) filming at 108 frames/s to provide at least three views of each attempt. Shutter speeds varied from ~4 to 6 ms, depending on light levels, and motion blur was minimal due to the abundant natural light. The cameras were arranged on two sides of a filming area (~3 × 3 × 2.5 m high) in the center of the greenhouse, and white curtains were extended on the other two sides to reduce background clutter in the videos.

We analyzed 162 trials in which dragonflies were pursuing fruit flies or mosquitoes (sample sizes of videos of houseflies and deerflies were insufficient for statistical analysis). We extracted 3D coordinates of (1) the perched dragonfly, (2) the position of the prey during the frame when dragonflies initiated pursuit (at take-off), and (3) the location of capture, using DLTdv5 in MATLAB (Hedrick 2008) with a custom wand-calibration routine. From the 3D coordinates and frame numbers, we calculated the time from take-off to capture, the linear distance between the perch and the capture location ($d_{capture}$; Fig. 1F), and the average pursuit velocity (capture distance/ capture time). We also calculated the initial distance and elevation angle (from the horizontal) of the prey relative to the dragonfly at take-off (d_{prey} and ϕ_{prey}, respectively; Fig. 1F). We chose to quantify the time and distance traveled from the perch to the capture location, rather than the total time and distance from take-off to landing for several reasons; the return trip (i.e., from the point of capture back to the perch) is meandering and variable between trials, often involves significant periods of gliding (and is thus difficult to relate to expenditure of energy), and is associated more with the handling of prey (shifting prey from the legs to the mouth) than to its capture.

Predation measures were analyzed using a two-way ANOVA in SPSS, with species of dragonfly and type of prey as fixed factors. Because several of the predation variables had a significant interaction between species of dragonfly and type of prey, we further explored the data by performing separate one-way ANOVAs for trials on fruit flies and mosquitoes (with species of dragonfly as the fixed factor), and by performing *t*-tests to compare fruit fly versus mosquito trials within each dragonfly species. Post hoc analyses of differences between dragonfly species were performed using a Fisher's least significant difference (LSD) test. Relationships between predation measures across all dragonflies and types of prey were assessed by calculating Pearson product–moment correlation coefficients (ρ) in SPSS.

Because these analyses revealed that the initial position of the prey at the time of dragonfly take-off was critical to the interaction, we performed further analyses to characterize the motion of the prey during the 100 ms prior to take-off, the period during which visual information is thought to be used by the dragonfly to determine whether or not to initiate pursuit (Olberg et al. 2005). We digitized the position of the prey in the 10 frames prior to dragonfly take-off and smoothed these data with a third-order Butterworth filter in MATLAB. We calculated average translational velocity of the prey during this period, as well as average angular velocity of the prey relative to the dragonfly (change in θ, the angle between successive dragonfly–prey vectors, divided by time; Fig. 1E). Finally, we estimated the

average visual angle subtended on the dragonfly's eye by the prey during this period, based on the distance to the prey and the size range of each prey type (Fig. 1E); visual angle was estimated for both the minimum and maximum size of each type of prey, and the average was used for statistical analysis. Because it was not possible to digitize the prey's motion prior to take-off in all videos, we binned trials of all species of dragonflies pursuing the same type of prey (fruit flies: $n = 76$; mosquitoes: $n = 38$; houseflies: $n = 13$; deerflies: $n = 4$), and compared variables measured in trials with fruit flies versus mosquitoes using a t-test in SPSS.

Results

Capture success

Average capture success of dragonflies preying on fruit flies was 91.9% for the small Ruby Meadowhawks (*S. rubicundulum*; number of trials, $n = 135$; number of individuals, $i = 18$), 97.1% for the intermediate-sized Blue Dashers (*P. longipennis*; $n = 104$, $i = 6$), and 89.5% and 93.1% for the larger Spangled and Painted Skimmers, respectively (*L. cyanea*, $n = 19$, $i = 2$; *L. semifasciata*, $n = 29$, $i = 3$; Fig. 2A). Capture success of dragonflies preying on mosquitoes was 75.9% for *S. rubicundulum* ($n = 29$, $i = 5$), 78.7% for *P. longipennis* ($n = 47$, $i = 9$), 70.0% for *L. cyanea* ($n = 20$, $i = 4$), and 66.7% for *L. semifasciata* ($n = 21$, $i = 4$). Capture success on houseflies was 66.7% for *S. rubicundulum* ($n = 24$, $i = 5$), and 56.3% for *P. longipennis* ($n = 16$, $i = 4$), and on deerflies was 20.0% for *L. cyanea* ($n = 15$, $i = 3$), and 42.9% for *L. semifasciata* ($n = 21$, $i = 3$). Success was significantly higher for all dragonfly species when preying on fruit flies versus mosquitoes (paired t-test, $P = 0.003$; Fig. 2A).

Capture efficiency

No significant differences were found among male and female dragonflies for any of the variables measured concerning efficiency of capture during pursuits of fruit flies (*S. rubicundulum*: $P > 0.05$ for all variables, one-way ANOVA; *P. longipennis*: $P > 0.05$ for all variables, Kruskall–Wallis test; *L. cyanea* and *L. semifasciata*: only females filmed) or during pursuits of mosquitoes (Kruskall–Wallis test: $P > 0.05$ for all variables in all species of dragonflies except *L. semifasciata*, in which only females were filmed).

Time to capture differed significantly among species of dragonfly and types of prey pursued (Table 1 and Fig. 3A). Within fruit fly trials, capture times were similar among all dragonfly species; however, dragonflies pursuing mosquitoes differed significantly

in capture time, with *L. semifasciata* requiring longer than *L. cyanea* (LSD test, $P = 0.027$) or *P. longipennis* ($P < 0.001$) to capture mosquitoes, and tending toward longer capture times than *S. rubicundulum* ($P = 0.072$). All species required longer to capture mosquitoes than to capture fruit flies, with significant differences in the two larger dragonflies (t-tests: *L. cyanea*, $P = 0.037$; *L. semifasciata*, $P = 0.001$), and similar trends in the smaller species (*S. rubicundulum*, $P = 0.061$; *P. longipennis*, $P = 0.064$).

Distance to capture differed significantly among types of prey, but not among dragonfly species (Table 1 and Fig. 3B). Most species traveled farther to capture mosquitoes than to capture fruit flies (t-tests: *P. longipennis*, $P = 0.010$; *L. semifasciata*, $P = 0.008$; *L. cyanea*, $P < 0.001$), with only the smallest dragonfly, *S. rubicundulum*, showing similar capture distances for the two types of prey (t-test, $P = 0.322$). Capture distance was strongly correlated with capture time ($\rho = 0.795$).

Average pursuit velocity differed among dragonfly species, but did not vary consistently with the type of prey pursued (Table 1 and Fig. 3C). When pursuing fruit flies, the large *L. cyanea* flew more slowly on average than all other species (LSD: *S. rubicundulum*, $P < 0.001$; *P. longipennis*, $P < 0.001$; *L. semifasciata*, $P = 0.009$). When pursuing mosquitoes, the intermediate-sized *P. longipennis* flew significantly faster than the small *S. rubicundulum* (LSD: $P = 0.006$) or large *L. semifasciata* ($P = 0.002$), and tended to fly faster than *L. cyanea* (LSD, $P = 0.061$). Within dragonfly species, both *P. longipennis* and *L. cyanea* flew significantly faster when pursuing mosquitoes versus fruit flies (t-tests: *P. longipennis*, $P = 0.017$; *L. cyanea*, $P < 0.001$), whereas the other two dragonfly species showed no significant difference. Average pursuit velocity was correlated with capture distance ($\rho = 0.463$), but not with capture time ($\rho = -0.103$).

Initial position and motion of prey

No significant differences were found among male and female dragonflies in initial distance to fruit flies or to mosquitoes ($P > 0.05$ for the same species/tests as for capture efficiency above), and only *P. longipennis* in pursuit of fruit flies had a significant difference between males and females in the angle of elevation of the prey ($P = 0.021$, Kruskall–Wallis test).

Initial distance to prey at the time of dragonfly take-off differed significantly among types of prey, but not among species of dragonfly (Table 1 and Fig. 4A). All dragonfly species initiated pursuit at greater initial distances when chasing mosquitoes as
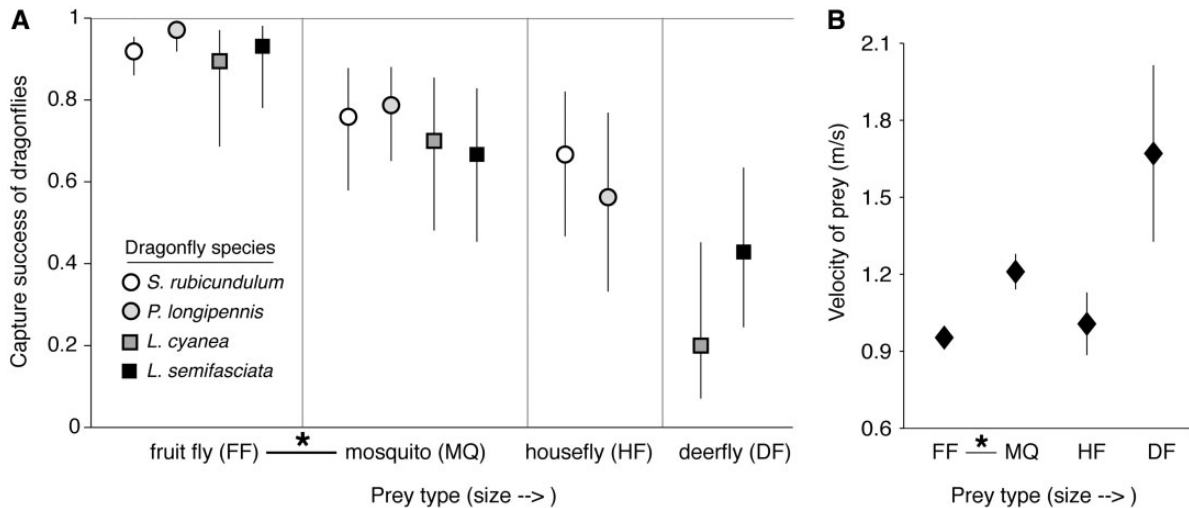
Fig. 2 Capture success of four species of dragonflies pursuing different types of prey, and average flight velocity of each prey type. Prey types are shown on the horizontal axis in order of increasing size; asterisks represent a significant difference among prey types (only tested for fruit fly and mosquito trials). (**A**) Capture success was calculated as the number of successful captures divided by the total number of attempts recorded for a given species of dragonfly (pooling all individuals) pursuing a particular type of prey. Bars represent 95% confidence intervals calculated using the Wilson score interval for binomial proportions. (**B**) Average velocity of each type of prey, calculated over the 102 ms prior to dragonfly take-off. Bars represent standard error (fruit fly: $n = 76$, mosquito: $n = 38$, housefly: $n = 13$, deerfly: $n = 4$).

Table 1 Results of ANOVA analyses performed on capture efficiency parameters and initial prey position

	Two-way ANOVA (dragonfly, prey)			ANOVA (fruit fly)	ANOVA (mosquito)
	Dragonfly	Prey	Dragonfly*Prey	Dragonfly	Dragonfly
Time to capture	$F = 8.718$, $P < 0.001$	$F = 26.975$, $P < 0.001$	$F = 3.428$, $P = 0.019$	$F = 1.623$, $P = 0.189$	$F = 4.980$, $P = 0.004$
Distance to capture	$F = 1.524$, $P = 0.211$	$F = 23.550$, $P < 0.001$	$F = 0.747$, $P = 0.526$	$F = 2.354$, $P = 0.077$	$F = 0.561$, $P = 0.643$
Pursuit velocity	$F = 8.711$, $P < 0.001$	$F = 2.260$, $P = 0.135$	$F = 5.091$, $P = 0.002$	$F = 7.665$, $P < 0.001$	$F = 5.088$, $P = 0.004$
Initial pray distance	$F = 1.424$, $P = 0.238$	$F = 57.607$, $P < 0.001$	$F = 2.661$, $P = 0.050$	$F = 3.979$, $P = 0.010$	$F = 1.131$, $P = 0.345$
Initial pray elevation	$F = 2.682$, $P = 0.049$	$F = 20.132$, $P < 0.001$	$F = 1.910$, $P = 0.130$	$F = 5.436$, $P = 0.002$	$F = 1.484$, $P = 0.229$

Two-way ANOVAs were performed with species of dragonfly and type of prey as fixed factors, as well as one-way ANOVAs testing the effect of dragonfly species within each prey type. Results that are significant at the $P = 0.05$ level are shown in bold.

compared to when chasing fruit flies (*t*-tests: *S. rubicundulum*, $P = 0.005$; *P. longipennis*, $P = 0.004$; *L. cyanea*, $P < 0.001$; *L. semifasciata*, $P < 0.001$). Within mosquito trials, there was no difference among species of dragonflies in initial prey distance; however, prey distance differed significantly among species of dragonflies during fruit fly trials, with the large *L. cyanea* pursuing fruit flies from shorter initial distances than did the two smaller dragonflies (LSD: *S. rubicundulum*, $P = 0.001$; *P. longipennis*, $P = 0.013$), and tending toward shorter initial distances than *L. semifasciata* (LSD: $P = 0.063$). Initial

prey distance was strongly correlated with capture distance ($\rho = 0.581$) and less strongly correlated with capture time ($\rho = 0.452$) and average velocity ($\rho = 0.301$).

Initial prey elevation angle relative to dragonflies at take-off differed both among species of dragonfly and among types of prey (Table 1 and Fig. 4B). Dragonflies generally initiated pursuit with prey at lower angles of elevation when chasing mosquitoes as compared to when chasing fruit flies, with significant differences among types of prey in *S. rubicundulum* and *L. semifasciata* (*t*-tests,
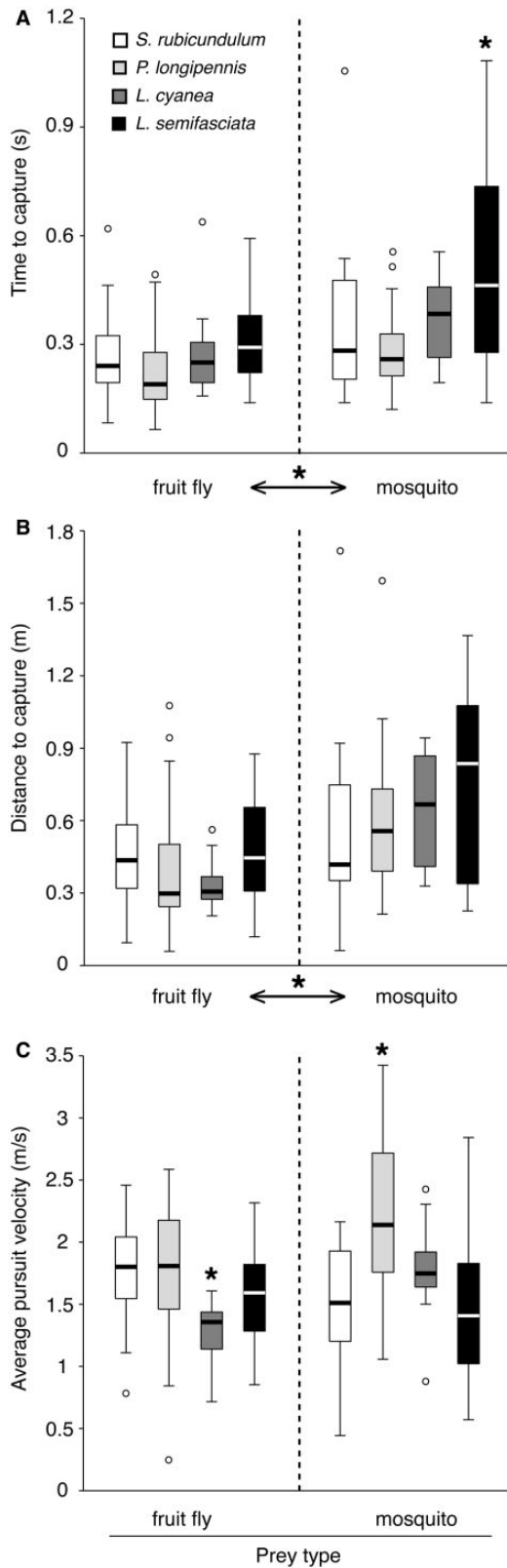
Fig. 3 Capture efficiency parameters measured from high-speed videos of dragonflies pursuing different types of prey. (A) Time to capture (time from dragonfly take-off to prey capture). (B) Distance to capture (linear distance between perch and capture point). (C) Average pursuit velocity (distance to capture/time to capture). Prey types are shown along the horizontal axis, with

S. rubicundulum, $P < 0.001$; *L. semifasciata*, $P = 0.018$). Within mosquito trials, there was no significant difference among species of dragonfly in initial prey elevation angle. However, within fruit fly trials, the small *S. rubicundulum* pursued fruit flies from higher initial prey elevation angles than all other dragonfly species (LSD: *P. longipennis*, $P = 0.002$; *L. cyanea*, $P < 0.001$; *L. semifasciata*, $P = 0.027$).

Prey velocity prior to dragonfly take-off was significantly higher for mosquitoes than for fruit flies (*t*-test, $P < 0.001$), with an average velocity of 1.21 ± 0.43 m/s for mosquitoes, as compared to 0.95 ± 0.27 m/s for fruit flies (Fig. 2B). However, angular velocity was significantly lower for mosquitoes as compared to fruit flies (*t*-test, $P = 0.002$; mean $\pm$ SD $= 204.8 \pm 157.3°$/s in mosquitoes, $324.0 \pm 203.0°$/s in fruit flies). The average visual angle subtended by the prey prior to take-off did not differ significantly between mosquitoes and fruit flies (*t*-test, $P = 0.503$; mean $\pm$ SD $= 1.1 \pm 0.7°$ in mosquitoes, $1.0 \pm 0.6°$/s in fruit flies).

Discussion

Effect of prey size on capture success and efficiency of dragonflies

We predicted that prey size would affect both capture success and capture efficiency of dragonflies, with larger prey being faster and more difficult to catch, and requiring longer flights that would take dragonflies farther from their perch. Our results show that dragonflies' capture success does decrease substantially with the size of prey in all four dragonfly species (Fig. 2A), and that the average velocity of prey generally increases with their size (Fig. 2B). Capture efficiency also decreases as predicted, with dragonflies taking more time and traveling farther from their perch when capturing larger mosquitoes, as compared to when capturing smaller fruit flies (Fig. 3A and B).

However, it is not clear that the greater distances and times required for capturing mosquitoes are due to the flight performance (e.g., speed or evasiveness) of the prey themselves, as we had predicted.

Fig. 3 Continued

significant differences among prey type indicated by an asterisk. Dragonflies are arranged in order of increasing body size; boxes show median and interquartile range (IQR), whiskers show the most extreme data point within 1.5*IQR of the nearest quartile, and circles are outliers. Within each prey type, species of dragonflies that differ significantly from others are indicated by an asterisk.
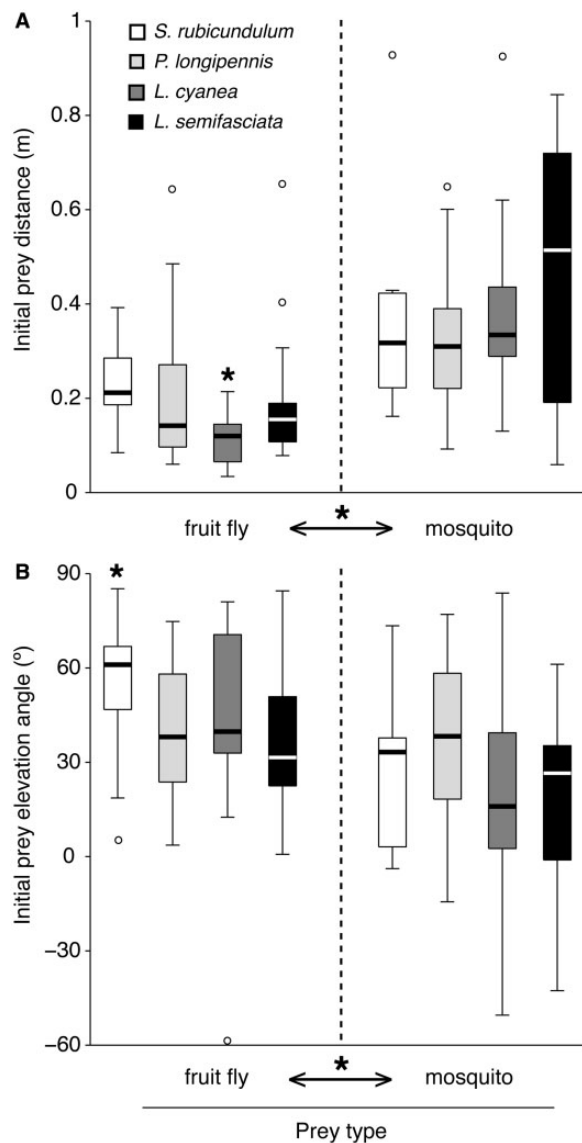
Fig. 4 Position of prey at the time of dragonfly take-off, measured from high-speed videos of dragonflies pursuing different types of prey. (**A**) Initial prey distance (linear distance from dragonfly to prey). (**B**) Initial elevation angle (from the horizon) of prey relative to perched dragonfly. Prey types are shown along the horizontal axis, with significant differences among prey type indicated by an asterisk. Dragonflies are arranged in order of increasing body size; boxes show median and IQR, whiskers show the most extreme data point within 1.5*IQR of the nearest quartile, and circles are outliers. Within each prey type, species of dragonflies that differ significantly from others are indicated by an asterisk.

Dragonflies initiated pursuits of mosquitoes from greater initial distances, as compared to pursuits of fruit flies, where the prey were closer on average (Figs. 4A and 5A). Distance to capture and time to capture were both correlated with initial distance between dragonfly and prey; thus, the reduced capture

efficiency of dragonflies pursuing mosquitoes may be more related to the initial conditions of the pursuit than to what occurred during the interaction. These initial conditions may be determined by a number of factors, including the dragonfly's ability to detect prey and its decision of whether or not to initiate pursuit, both of which may be affected by the prey's size, velocity, and location.

If a dragonfly's decisions about whether or not to pursue prey were based solely on minimizing the costs associated with predation (i.e., avoiding energetically wasteful, failed attempts), we might expect a trend opposite to what was observed: dragonflies would only pursue larger (and presumably quicker and more evasive) prey when the prey passed relatively close to their perch (making success more likely), but would be less choosy about the initial distance to smaller, slower prey that are relatively easy to catch. However, if a dragonfly's decisions about initiating pursuit were based on maximizing the potential rewards of predation (i.e., increasing energetic intake by capturing significantly larger prey), then our results could point to adaptive behavior on the part of the dragonfly; dragonflies may choose to pursue larger prey whenever presented with the opportunity (even if prey are farther away and success is less likely) because the potential reward is much greater, but reject small prey that are farther away and not worth the risk of failure.

An alternative hypothesis to explain the observed patterns is that initial prey distances are driven not by dragonflies' decisions about whether or not to initiate a pursuit based on potential costs or rewards, but by their ability to detect and identify moving objects as likely targets for predation. Dragonflies' eyes contain several functionally distinct zones, including a dorsal acute zone (located ~60° above the horizon in many libellulid dragonflies) (Labhart and Nilsson 1995; Olberg et al. 2007), which is characterized by high spatial acuity for tracking small targets against a blue sky. However, a consequence of high spatial acuity can be a tendency toward motion blur, particularly of relatively large (e.g., close), fast objects moving across the visual field (Land 1997). Thus, a larger (and presumably faster) mosquito flying close to a dragonfly could induce motion blur and fail to be identified as a distinct target (Olberg 1986; Frye and Olberg 1995; Gonzalez-Bellido et al. 2013), placing a lower limit on detection distance that depends on the prey's size and speed. Although we cannot rule out motion blur as a contributing factor, our measurements of the angular velocity of prey suggest that this is not responsible for the observed patterns; angular velocities
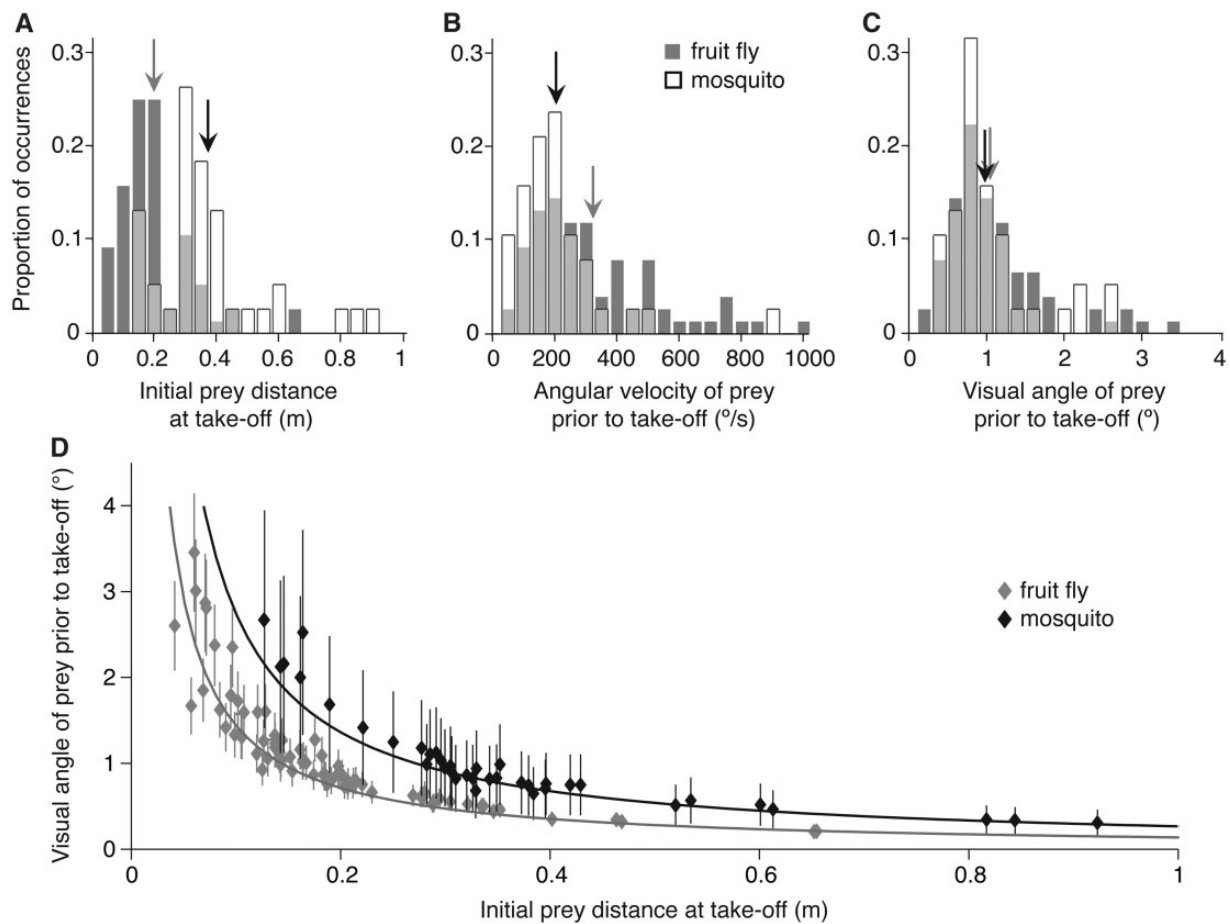
Fig. 5 Angular velocity, visual angle, and initial distance of prey relative to perched dragonflies. (**A–C**) Distributions of prey variables for fruit fly and mosquito trials, pooled over all species of dragonflies. (A) Initial distance to prey at the time of dragonfly take-off was significantly higher in mosquitoes (mean = 0.37 m, black arrow) than in fruit flies (mean = 0.20 m, gray arrow; t-test, $P < 0.001$). (B) Angular velocity of prey prior to dragonfly take-off was significantly lower in mosquitoes (mean = 204.8°/s) than in fruit flies (mean = 324.0°/s; t-test, $P = 0.002$). (C) Visual angle subtended by the prey prior to dragonfly take-off was not significantly different among mosquitoes (mean = 1.0°) and fruit flies (mean = 1.1°; t-test, $P = 0.582$). (D) Visual angle subtended by the prey prior to dragonfly take-off versus initial prey distance at the time of take-off. Symbols represent average visual angle, and bars show estimated maximum and minimum visual angle, based on the size range of each type of prey. Visual angle of prey in the 102 ms preceding take-off declines approximately as d_{prey}^{-1}, with an intercept equal to the arctangent of prey length (black and gray curves).

of fruit flies were in fact significantly higher than those of mosquitoes (Fig. 5B), and thus the greater velocity of mosquitoes does not appear to limit the minimum prey distance at take-off.

However, the relationship between initial prey distance at dragonfly take-off and the average visual angle of prey prior to take-off (Fig. 5D) suggests that the visual angle subtended on the dragonfly's eye may become too large when mosquitoes are flying close to the perch. Dragonflies rarely pursued prey that subtended an angle greater than 3°, and appeared to have a strong preference for visual angles of about 1° (Fig. 5D), with very similar distributions of visual angle in trials with fruit flies and mosquitoes (Fig. 5C), despite the difference in prey size.

These empirical measurements fit well with previous studies of dragonflies' visual neurobiology, which show that neurons involved in detection and pursuit of targets are most sensitive to visual angles of 1–4°. In the optic ganglion of the dragonfly's brain, one particular class of neurons (small target motion detectors, or SMTDs) responds most strongly to targets subtending visual angles of 1–2°, with responses dropping off rapidly at angles greater than 3–4° (O'Carroll 1993). Another class of neurons, the target-selective descending neurons (TSDNs), descend from the brain to the thoracic ganglia and respond selectively to small (1–4°) visual targets, with direct stimulation leading to changes in wing position that may be related to pursuit behavior (Olberg et al. 2000). Thus, it is likely that prey that

are large enough and close enough to subtend a visual angle greater than ∼3–4° would not be detected by these neurons, and therefore would not be pursued by the dragonfly.

These results imply that dragonflies may be missing out on some of their easiest (and potentially most rewarding) meals, by allowing prey that fly very close to their perch, and that could therefore be caught very quickly, to pass by. Small prey may rarely fly close enough (within a few centimeters) to be undetectable to a perched dragonfly, but larger prey, which would be undetectable within 10–20 cm of the perch, may benefit from this visual glitch. This may also contribute to the lower capture success of dragonflies pursuing large prey, as the greater initial distances at the start of these pursuits would compound the difficulty of capturing larger, faster prey.

Conversely, at greater distances from the perched dragonfly, small prey may no longer be detectable by the dragonfly's visual system, placing an upper limit on the distance at which they can be detected. This may be reflected by the fact that dragonflies in our study initiated far more pursuits from long initial distances (e.g., 0.5–1.0 m) when chasing mosquitoes than when chasing fruit flies (Figs 4A and 5).

Capture success and efficiency of different dragonfly species

In comparing the capture success and efficiency of different species of dragonflies, we anticipated several potential outcomes, including (1) similar performance among all dragonflies (if interactions are driven by behavior of the prey), (2) scaling of performance with the size of dragonflies (if flight speed or other traits that scale with body size are important), or (3) evidence that certain species of dragonflies are specialized for capturing particular types of prey (if non-size-related aspects of flight performance or behavior are important).

We found that capture success is indeed similar among all four species of dragonflies when pursuing a given type of prey (i.e., there are greater differences in capture success among types of prey than among dragonfly species; Fig. 2A), which suggests that the flight performance and behavior of the prey play a key role in determining the ultimate outcome of dragonfly–prey interactions. However, the way in which these captures were effected (e.g., initial position of prey, time and distance to capture, and velocity of pursuit) varied among species of dragonflies, suggesting some degree of specialization.

Libellula semifasciata, one of the larger species tested, took significantly longer to capture mosquitoes than did other dragonflies, and in general showed high variability and poor performance when pursuing mosquitoes (e.g., highest initial prey distances and capture distances, lowest average pursuit velocities, and lowest capture success). The other large species, *Libellula cyanea*, displayed a significantly lower average pursuit velocity than did the other dragonflies when chasing fruit flies (Fig. 3C), and a slightly lower capture success (although success was still quite high; Fig. 2A). The low pursuit velocity of these chases may be related to the fact that *L. cyanea* initiated pursuit of fruit flies when the prey were significantly closer, as compared to other dragonflies (Fig. 4A), resulting in relatively low capture distances—yet, these captures required approximately the same total time as for other species that traveled further (Fig. 3A). This species also displayed some of the most consistent capture behavior, with low variability in initial distance to prey and average pursuit velocity for both types of prey, as well as in the distance required to capture fruit flies. It is possible that the low average pursuit velocities and short capture distances displayed by *L. cyanea* when pursuing fruit flies reflect a strategy for maximizing energetic efficiency and/or remaining close to their perch, thereby maintaining dominance over important territories.

The intermediate-sized species, *Pachydiplax longipennis*, is aptly named the "Blue Dasher"; it had significantly higher average pursuit velocities than did other species when chasing mosquitoes, and one of the two highest pursuit velocities when chasing fruit flies (Fig. 3C), suggesting that its initial acceleration may be higher than that of the other dragonflies. This species also had the lowest median capture times when pursuing both types of prey (Fig. 3A), and it captured fruit flies in the shortest distance (despite the fact that *L. cyanea* appears to wait for fruit flies that approach more closely; Fig. 3B). Thus, *P. longipennis* displayed the best overall performance in terms of "capture efficiency" (although not necessarily energetic efficiency), by minimizing both the time required and distance traveled from its perch to capture prey.

More generally, our results suggest that average pursuit velocity may be a useful indicator of capture success, at least for dragonflies pursuing smaller prey such as fruit flies and mosquitoes. Species of dragonflies that displayed higher average velocities when pursuing these prey (e.g., *P. longpennis*) tended to have the greatest success, and those with lower pursuit velocities (e.g., *L. cyanea* pursuing fruit flies and

L. semifasciata pursuing mosquitoes) tended to have the least success (Fig. 2). In addition, there is a rather strong linear relationship between capture success and average pursuit velocity in trials both with fruit flies and mosquitoes, with a similar slope for each type of prey (fruit flies: $y = 0.110 \; x + 0.749$, $r^2 = 0.535$; mosquitoes: $y = 0.117 \; x + 0.530$, $r^2 = 0.478$).

Finally, our estimates of capture success across a range of prey types lend support to the idea that some species of dragonflies may be specialized for pursuing particular types of prey. For example, although *P. longipennis* exhibited greater capture success when pursuing fruit flies and mosquitoes than did other dragonflies, the success of *P. longipennis* with houseflies (based on a limited sample size of 16 pursuits) was lower than that of the smaller *S. rubicundulum* ($n = 24$; Fig. 2). Field studies of foraging behavior in *P. longipennis* also support the idea that this species is specialized for feeding on relatively small prey; these dragonflies are rarely observed pursuing insects larger than a few milligrams (∼9% of prey taken), despite the fact that they are capable of capturing larger prey, and the fact that a similarly sized species in the same habitat (*Erythemis simplicollis*) routinely captures larger prey (∼41% of prey taken) (May and Baird 2002).

Conclusions

Nearly all parameters measured concerning dragonfly prey-capture success and efficiency varied significantly with the type of prey pursued, and differences due to the type of prey were generally greater than those due to the species of dragonfly. Prey type appears to determine most gross features of the interaction, including the distance to prey at the time of dragonfly take-off, average time and distance of the pursuit, and capture success. However, the relative contributions of dragonfly predatory traits (e.g., sensory capabilities, pursuit decisions) and prey flight characteristics (e.g., size, speed, erratic flight, evasiveness) in determining these overall features of predator–prey interactions remain unresolved, and thus it is difficult to extend conclusions drawn from studying dragonflies pursuing one prey type to their interactions with different prey.

One particularly important question that needs to be addressed is whether some types of prey regularly respond to approaching dragonflies by performing evasive maneuvers—as opposed to fruit flies, which are typically unresponsive and only rarely alter their flight patterns as dragonflies approach (Combes et al. 2012). Our preliminary analysis of 3D flight trajectories of dragonflies pursuing larger prey such as houseflies suggest that these prey do actively maneuver, and are often able to evade the dragonflies several times before the dragonflies either capture them or give up and return to their perch. Dragonflies that tend to pursue nonresponsive prey such as fruit flies might adopt different pursuit strategies and be specialized for different aspects of flight performance (e.g., rapid acceleration and predictive interception of the target), as opposed to species that frequently pursue evasive prey, for which careful control of flight speed, rapid response times, and high maneuverability/agility might be more beneficial. Thus, without resolving these questions of variability in prey behavior and the specializations of dragonflies for particular types of prey, it is also difficult to extrapolate results of predation studies performed on one species of dragonfly to another, even among closely related species residing in the same habitat.

Overall, our results underscore the importance of performing comparative studies of predator–prey interactions with freely behaving subjects in natural settings, to provide insight into how the locomotory capabilities and behavior of both participants influence the dynamics of the interaction. In addition, it is clear that gaining a full understanding of these interactions requires detailed knowledge not only of locomotory mechanics and behavior, but also of the sensory capabilities and constraints of both predator and prey.

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