



Prey selection by dragonflies in relation to prey size and wasp-like colours and patterns

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Although most of the studies on the evolution of mimicry and warning signals in insects have considered birds as the main predators, predation by other taxonomic groups, such as insects, may far exceed avian predation at some localities. However, few studies have investigated the possibility that insect predators might facilitate selection for warning colours and mimicry in other insects. We experimentally evaluated whether prey size and/or wasp-like colours and patterns were important in deterring attacks by dragonflies, using pairwise and single presentations of both natural and artificial prey in the field. Dragonflies were more likely to attack smaller natural prey and smaller artificial prey. However, dragonflies showed no differences between attacks on prey with wasp-like colours and patterns and those on the same-sized prey that were nonmimetic. Moreover, dragonflies avoided attacking both mock-painted and black-painted wasps entirely. Overall, we found no evidence to support the hypothesis that wasp-like warning signals protect small insect prey from attack by dragonflies, although size seems to be an important cue in dragonfly prey choice.

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I never saw the flocks of slow-flying Heliconidae in the woods persecuted by birds or Dragonflies, to which they would have been easy prey; nor, when at rest on leaves, did they appear to be molested by Lizards or the predacious Flies of the family Asilidae, which were very often seen pouncing on Butterflies of other families (H. W. Bates 1862, page 510).

Despite Bates' observations that insect predators may selectively refrain from attacking certain types of prey, birds have long been considered as the primary selective agent involved in the evolution of warning signals (Poulton 1890; Guilford 1990) and mimicry (Bates 1862; Müller 1878; Mallet & Joron 1999) in insects and other invertebrates. Indeed, given the widespread occurrence of visually hunting insects such as wasps, robber flies and dragonflies, it is remarkable that so few studies have examined the role of such predators in shaping the evolution and maintenance of protective coloration. Shelly & Pearson (1978) suggested that predatory robber flies (Diptera: Asilidae) may have been responsible in part for the

evolution of conspicuous warning signals in chemically defended tiger beetles. A study by Dejean (1988) revealed that hunting workers of an ant species, *Odontomachus troglodytes*, avoided attacking the chemically defended and warningly coloured larvae of African chrysomeline (Coleoptera: Chrysomelidae) for 28 days after their initial encounter. In perhaps the first formal experimental study of its kind, Berenbaum & Miliczky (1984) found that the Chinese mantid *Tenodera ardifolia sinensis* rapidly learned to avoid unpalatable milkweed bugs, *Oncopeltus fasciatus*, that had been reared on milkweed seeds. Furthermore, of six mantids that had learned to reject milkweed-fed bugs, none attacked palatable sunflower-fed bugs when they were offered. Bowdish & Bultman (1993) confirmed that this species of mantid could learn to avoid attacking unpalatable milkweed bugs, but also found that the mantids attacked natural and stripe-painted milkweed bugs overall less frequently than they did black-painted bugs, which may more closely resemble palatable flies. Thus, Berenbaum & Miliczky (1984) showed that invertebrate predators may facilitate selection for mimicry, and Bowdish & Bultman (1993) showed that invertebrate predators could also generate selection in unpalatable prey to evolve particular forms of warning signals.

Most recently, Kauppinen & Mappes (2003) evaluated the responses of the dragonfly *Aeshna grandis* to encounters with black natural prey, warningly coloured natural

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prey (painted flies and wasps) and artificial prey in the field. These prey items were presented to the dragonflies singly, using a fishing rod and line. After observing behavioural responses of the dragonflies towards the prey (e.g. pause but do not touch, touch but do not grab), the authors concluded that black-and-yellow striped flies were 'avoided more' than were black ones and suggested that wasp-like coloration may confer a selective advantage against odonate predators.

The purpose of this study was to continue to address the shortfall of observations on foraging preferences by insects in the context of the evolution of protective coloration, particularly warning signals and mimicry. Similar to [Kauppinen & Mappes's \(2003\)](#) study, we examined prey selectivity by adult dragonflies in the field. As Kauppinen & Mappes noted, adult dragonflies are an excellent model group of invertebrate predators for such studies because they are voracious, have well-developed visual systems ([Yang & Osorio 1991](#); [Briscoe & Chittka 2001](#)) and feed on a variety of arthropod prey ([Corbet 1999](#)). As Bates observed more than 140 years ago, dragonflies do not always attack prey items that they approach (see also [Beatty 1951](#); [Baird 1991](#)). For example, [O'Donnell \(1996\)](#) found that Neotropical dragonflies oriented towards wasps but rarely pursued them, and suggested that such behaviour may potentially select for warning signals and mimicry.

Although we have independently used a similar approach to that used by [Kauppinen & Mappes \(2003\)](#), our study complements that by Kauppinen & Mappes in several ways. First, we scored responses of several species of (principally libellulid) dragonflies, rather than a single predator species. We chose not to focus on an individual odonate species, because natural prey are exposed to a variety of dragonfly predators. Second, we scored dragonfly responses to artificial and natural prey including hover flies; Kauppinen & Mappes presented no natural mimics. Third, unlike Kauppinen & Mappes, who admirably controlled for prey size, we explicitly tested the possibility that dragonflies may be size selective. Fourth, we think that studies aimed at elucidating the advantages of protective coloration require an assessment of the frequency of encounters of predators with different prey types, as well as the nature of predatory behaviour following encounter. Thus, we allowed for potential differences in conspicuousness between prey types by presenting two prey types simultaneously along different ends of a rod, as well as conducting single presentations and recording nonencounters.

METHODS

Our experiments were conducted in two adjoining open meadows (combined area approximately 1.5 ha) near the Queen's University Biological Station, Ontario, Canada (44°34'N, 79°15'W). All prey-choice experiments were performed from 5 June to 10 August in 2003 and 2004, on sunny days during 1100–1530 hours. Air temperature during experiments ranged from 28 to 33°C; humidity ranged from 70 to 80%. We conducted weekly surveys of dragonflies from mid-June to early August 2004 to

identify the adult dragonfly species present in the meadows at the time of the study. Each survey lasted 2 h and involved an observer walking slowly around the edge of the meadows (where dragonflies tended to perch), and tallying the number of each dragonfly species seen. These surveys allowed us to estimate the presence and relative abundance of potential predator species during our experiments.

Two Malaise traps were set up in the meadows to assess the types and relative proportion of prey items naturally available to our dragonfly predators. These traps were emptied and the contents stored every 5 days from 1 July to 10 August 2004. We recognize that Malaise traps may provide at best a biased sample of the insect community present ([Southwood 1978](#)), but they allowed us to ascertain the extent to which various aerial prey species, more or less equally susceptible to trapping, were available to the dragonflies.

Our experiments were of three main types ([Table 1](#)). Each replicate of each experiment (16–60 replicates; [Table 1](#)) consisted of presenting dragonflies encountered in the field with different types of natural or artificial prey. Prey were tethered, pairwise or singly, on 50-cm cotton strings suspended from the end of an L-shaped rod with a 122-cm handle and a 76-cm support arm. Prey presented in pairs were attached 50 cm apart on the same support arm.

To present 'prey', an experimenter walked the perimeter of the field with the rod held in front and the support arm horizontal, so that the suspended prey were approximately 1–1.5 m above the ground. The rod was moved slowly from side to side and up and down to mimic the movement of natural prey. If dragonflies in the proximity made no response, then the experimenter continued walking around the perimeter of the field, presenting the prey to the next dragonfly encountered. Dragonflies frequently attacked natural or artificial prey while the experimenter was simply walking with the rod (50–70% of attacks); the remainder took place while prey were held in the proximity of dragonflies, with the experimenter standing still. After an attack occurred, the experimenter moved to another part of the field to minimize the probability of testing the same dragonfly twice and performed the next replicate (dragonflies were extremely abundant, and the probability of repeated attack was judged to be extremely small).

Natural prey items used in these experiments were collected by hand nets from within our field sites. In all experiments, the presented items were replaced with fresh specimens (either with natural colours and patterns or with painted colours and patterns) of the same species immediately after an attack or, if no attack occurred, after 8 min. To avoid bias in pairwise presentations, we switched the position of the two prey on the rod after each replicate. Similarly, the prey types presented singly in an experiment were always presented at the same time by different researchers who swapped the prey type they were presenting after each replicate. Presentations continued until a prey item was attacked (measured as a physical grasp) or until 8 min elapsed. If an attack was made, we recorded the prey type, predator species and duration of attack up to a maximum of 4 min (dragonflies often remained suspended on the string consuming natural prey). All of the natural potential

Table 1. A summary of the prey types offered and number of replicates in each experiment

Experiments	Prey types	Presentation method	Number of replicates
1–3 (large vs small prey (all black-grey))	(1) <i>Helicobia rapax</i> vs <i>Sarcophaga</i> spp.*	Pairwise	16
	(2) Large artificial prey vs small artificial prey	Pairwise	21
	(3) Large artificial prey vs small artificial prey	Single	30+30
4–7 (mimetic vs nonmimetic prey)	(4) <i>Toxomerus geminatus</i> (mimetic hover fly) vs <i>H. rapax</i>	Pairwise	38
	(5) Black-painted <i>Eristalis transversa</i> vs mock-painted <i>E. transversa</i>	Pairwise	47
	(6a) Black-and-yellow-striped artificial prey vs black artificial prey (2003)	Pairwise	30
	(6b) Black-and-yellow-striped artificial prey vs black artificial prey (2004)	Pairwise	52
	(7) Black-and-yellow-striped artificial prey vs black artificial prey	Single	30+30
8–9 (model vs mimic)	(8) Black-painted <i>Dolichovespula arenaria</i> vs mock-painted <i>D. arenaria</i>	Pairwise	20
	(9) <i>Dolichovespula arenaria</i> vs <i>T. geminatus</i>	Pairwise	20

*The majority of the *Sarcophaga* flies were identified as *S. bullata* (Parker).

prey used in our experiments were abundant at the experimental site (Table 2) and were tethered alive; they often attempted to fly when tied to the string, although they were clearly restricted in movement.

Water-based colours (Ultra Gloss acrylic enamel, DecoArt, Stanford, Kentucky, U.S.A.) were used to paint artificial prey types and natural prey items as required. A fine-bristled paintbrush was used to paint different prey types (artificial and natural). Mock-painted hover flies and wasps received a similar amount of paint as individuals in their comparison groups, but were painted so that they retained much of their former appearance (yellow stripes and patches on the thorax and abdomen were painted yellow; black segments and areas were painted black). Although the paints used were not different from the natural coloration of wasps to our eyes, we measured the reflectance of both the black and yellow paints using an Ocean Optics USB2000 spectrometer (Dunedin, Florida, U.S.A.) and a 200- μ m reflection probe at a 45° angle from the sample surface. Illumination was provided via a pulsed xenon (PX-2) light source. Spectra were recorded at 1-nm intervals from 350 to 700 nm and measured relative to a Labsphere 98% reflection standard (OOIrrad software version 2.04, Ocean Optics). The peak reflectance for the yellow paint was around 610 nm and the black paint showed a flat curve. These measurements are very close to those observed in vespid wasps (Kauppinen & Mappes 2003), which are considered to be the model for the mimetic hover flies. We detected no ultraviolet (UV) reflectance in our paints.

Large versus Small Prey (Experiments 1–3)

We conducted three experiments to examine whether dragonflies were size selective. We used pairwise presentations of small natural prey (*Helicobia rapax*) and larger natural prey (*Sarcophaga* spp.) (experiment 1), pairwise presentations of artificial prey of different sizes (experiment 2), and single presentations of artificial prey of different sizes (experiment 3). For the first experiment, the

Sarcophaga spp. presented ranged from 13 to 15 mm in total body length and the *H. rapax* ranged from 5 to 7 mm. Members of these fly genera are naturally grey-black and are not considered wasp mimics. For pairwise and single presentations of artificial prey, the small prey consisted of two ellipsoid plastic beads, each 3 × 4 mm (diameter × length), and the large prey consisted of two ellipsoid beads, one 3 × 4 mm and the other one 6 × 11 mm. The two beads used for each prey type were attached using a piece of wire as a central axis. We chose to use the above dimensions and shape to mimic the general size and shape of a potential natural prey as closely as possible. In these latter two experiments, the artificial prey were painted black (Table 1).

Mimetic versus Nonmimetic Prey (Experiments 4–7)

We then performed a series of four experiments to determine whether dragonflies were less likely to attack prey with wasp-like colours and patterns, while controlling for prey size. For experiment 4, we made pairwise presentations of natural mimics (*T. geminatus*) and nonmimetic flies of the same size (*H. rapax*). Although *T. geminatus* and *H. rapax* are similar in size (6–7 mm and 5–7 mm long, respectively), only *T. geminatus* resembles a wasp in many attributes except body size (as above). For experiment 5, we used individuals of a larger syrphid species, *Eristalis transversa* (11–12 mm in body length). This wasp mimic was relatively common at our study site and was selected as an experimental species because it was large enough to be painted with relative ease. Using pairwise presentations, we evaluated the attack responses of dragonflies to mock-painted individuals of *E. transversa* and conspecifics that were painted entirely black (nonmimetic). For experiments 6 and 7, we compared dragonfly responses to pairwise and single presentations of nonmimetic (black-painted) versus wasp-like (black-and-yellow-painted) artificial prey of the same size (diameter ×

Table 2. A summary of the flying insects collected in Malaise traps at our study site from 1 July to 10 August 2004

Order	Family	Percentage (by number)	Percentage of the insect order (by number)	Standard error (N=9 samples)
Diptera		52.58		7.69
	Tabanidae		54.58	8.91
	Bombyliidae		9.34	1.97
	Sarcophagidae			
	<i>Sarcophaga</i> spp.		6.1	1.31
	<i>Helicobia rapax</i>		5.15	1.47
	Asilidae		1.36	0.3
	Syrphidae			
	<i>Syritta</i> sp.		1.95	0.96
	<i>Syrphus rebesii</i>		0.39	0.19
	<i>Toxomerus geminatus</i>		10.12	2.04
<i>Eristalis</i> spp.		0.37	0.19	
Others		10.48	3.87	
Lepidoptera		35.56		8.26
	Hesperiidae			
	<i>Euphyes</i> sp.		23.89	6.34
	<i>Thymelicus</i> sp.		52.07	6.21
Others		23.76	5.78	
Hymenoptera		11.6		5.36
	Black-and-yellow wasps (including Vespidae)		11.55	1.94
	Other wasps		41.39	8.81
	Bees		47.04	9.16
Orthoptera		0.04		0.024

length = 3×8 mm). Artificial prey consisted of two attached beads (each 3×4 mm). To make the artificial prey a wasp mimic, we applied three stripes of yellow paint, approximately 1 mm wide (one on the first bead and two on the second bead), on a black-painted prey. We conducted two separate runs of experiment 6 using pairwise presentations of artificial prey: one in 2003 (experiment 6a) and one in 2004 (experiment 6b). In experiment 7, we presented each type of artificial prey singly.

Model versus Mimic Prey (Experiments 8, 9)

In our final two experiments, we tested the attack responses by dragonflies to mock-painted wasps, *Dolichovespula arenaria* (body length = 14–15 mm), and wasps painted black (nonmimetic) in pairwise trials (experiment 8) and to small mimetic hover flies, *T. geminatus*, and large wasps, *D. arenaria*, in pairwise trials (experiment 9).

RESULTS

Weekly surveys revealed that the most common dragonflies present in the field were *Sympetrum* spp. (meadowhawks), *Libellula luctuosa* (widow skimmer), *L. pulchella* (twelve-spotted skimmer), *L. quadrimaculata* (four-spotted skimmer), *Plathemis lydia* (common whitetail), *Leucorrhinia intacta* (dot-tailed whiteface), *L. proxima* (red-waisted whiteface), *Erythemis simplicicollis* (eastern pondhawk), *Aeshna canadensis* (Canada darner), *Anax junius* (common green darner), *Ladona julia* (chalk-fronted corporal) and *Pachydiplax longipennis* (blue dasher) (Corbet 1999). Data collected from the Malaise traps on nine occasions

indicated that the flying insect community at the experimental site included nonmimetic and mimetic flies, as well as wasps and bees (Table 2).

Large versus Small Prey (Experiments 1–3)

Dragonflies preferred small prey over large prey. In experiment 1, using small *H. rapax* flies and large *Sarcophaga* spp. flies, dragonflies attacked the *Helicobia* in 15 of 16 pairwise presentations (sign test: $P = 0.0005$; Fig. 1). In experiment 2, using nonmimetic small and large artificial prey, dragonflies attacked the smaller prey in 19 of 21 pairwise presentations (sign test: $P = 0.0002$; Fig. 1). In experiment 3, in which nonmimetic small and large artificial prey were presented singly in an 8-min period, dragonflies attacked small prey in 26 of 30 trials and attacked large prey in 8 of 30 trials (G test: $G_1 = 23.75$, $P < 0.001$; Fig. 1). Furthermore, for the subsets of small and large prey that were attacked, the median time to attack was significantly shorter for smaller than for larger prey (Mann-Whitney U test: $U = 52.5$, $N_1 = 26$, $N_2 = 8$, $P = 0.03$).

Mimetic versus Nonmimetic Prey (Experiments 4–7)

Dragonflies did not avoid wasp-like colours and patterns. In experiment 4, we recorded a nonsignificant tendency for dragonflies to attack *T. geminatus* wasp mimics (23 of 38 pairwise presentations) more than similar sized nonmimetic *H. rapax* flies (15 of 38 pairwise presentations; sign test: $P = 0.25$; Fig. 2). Furthermore, we

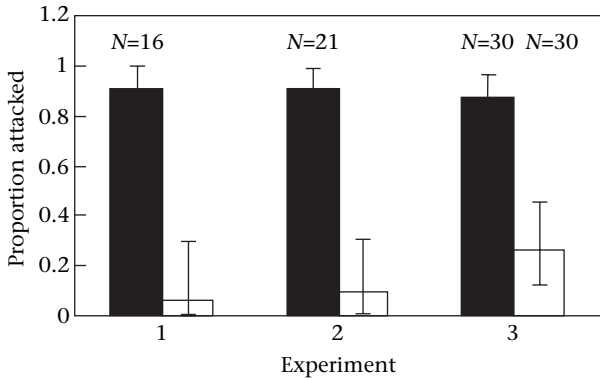


Figure 1. Proportion of attacks by dragonflies on small (■) and large (□) prey types in experiments 1–3. Experiment 1: *Helicobia rapax* and *Sarcophaga* spp. Experiment 2: pairwise presentations of artificial prey. Experiment 3: single presentations of artificial prey. Error bars indicate the exact binomial 95% confidence intervals.

found no difference between the median times that dragonflies spent feeding on hover flies and on nonmimetic flies (Mann–Whitney U test: $U = 147$, $N_1 = 23$, $N_2 = 15$, $P = 0.46$).

In experiment 5, using mock-painted and black-painted *E. transversa*, dragonflies directed 24 first attacks at mock-painted hover flies and 23 first attacks at individuals of the same species painted to look nonmimetic (sign test: $P = 1$; Fig. 2). In both experiments 6a (2003) and 6b (2004), dragonflies attacked black-painted artificial prey and yellow-and-black-painted artificial prey at approximately the same rates (experiment 6a: 14 versus 16, respectively; sign test: $P = 0.85$; experiment 6b: 30 versus 22, respectively; sign test: $P = 0.33$; Fig. 2). Similarly, in experiment 7 (single presentations of artificial prey during 8-min trials), dragonflies attacked black artificial prey in 28 of 30 trials and attacked yellow-and-black artificial prey in 27 of 30 trials (G test: $G_1 = 0.22$, $P = 0.64$; Fig. 2). The duration before the attacks also did not differ significantly

between black-and-yellow versus black artificial prey (Mann–Whitney U test: $U = 358$, $N_1 = 28$, $N_2 = 27$, $P = 0.73$).

Model versus Mimic Prey (Experiments 8, 9)

In experiment 8, neither black-painted nor mock-painted wasps, *D. arenaria*, were attacked in any of the 20 pairwise 8-min trials. However, in experiment 9, when dragonflies were presented with a choice of a wasp, *D. arenaria* and a hover fly, *T. geminatus*, they took only hover flies (20 attacks out of 20 pairwise presentations).

Dragonfly Species Selectivity

Overall, we observed a significant positive correlation between the mean proportion of times that a given dragonfly species was recorded in surveys and the proportion of attacks that species made during our experiments (Spearman rank correlation: $r_s = 0.724$, $N = 14$, $P = 0.003$; Fig. 3). We also conducted a series of chi-square tests to evaluate whether certain prey types (such as hover flies or flies) were attacked more frequently by certain size classes and/or species of dragonflies in our pairwise experiments. To do so, we categorized dragonfly species by total body length: small-size, 25.4–41 mm: *Celithemis eponina*, *Leucorrhinia intacta*, *L. proxima* and *Sympetrum* spp.; and medium, 43–51 mm: *Gomphus* sp., *Ladona julia*, *Libellula luctuosa*, *L. pulchella*, *L. quadrimaculata*, *Pachydiplax longipennis* and *Plathemis lydia*. We did not observe any attacks from large-sized dragonflies in the pairwise experiments. In experiments 4 (*T. geminatus* versus *H. rapax*) and 5 (*E. transversa*), there was no relation between small and medium dragonfly size classes and the type of prey they attacked (chi-square test: experiment 4: $\chi^2_1 = 0.008$, $P = 0.927$; experiment 5: $\chi^2_1 = 0.508$, $P = 0.476$). We analysed the results of experiments 6a (black-and-yellow

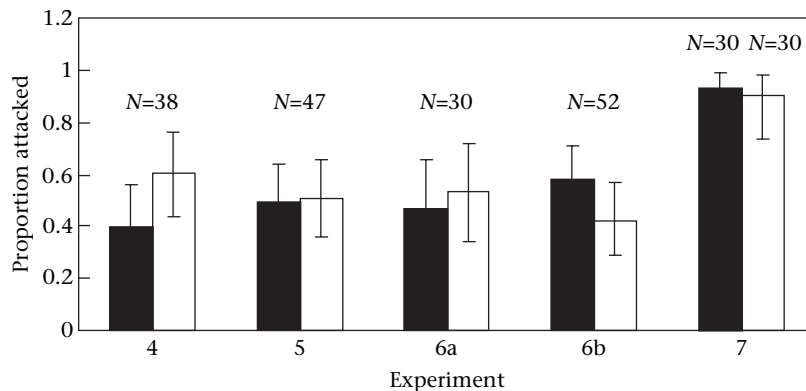


Figure 2. Proportion of attacks by dragonflies on mimetic (■) and nonmimetic (□) prey types in experiments 4–7. Experiment 4: pairwise presentations of mimetic *Toxomerus geminatus* and nonmimetic *Helicobia rapax*. Experiment 5: pairwise presentations of mock-painted and black-painted *Eristalis transversa*. Experiments 6a (2003) and 6b (2004): pairwise presentations of black-and-yellow-painted and black-painted artificial prey. Experiment 7: single presentations of black-and-yellow-painted and black-painted artificial prey. Error bars indicate the exact binomial 95% confidence intervals.

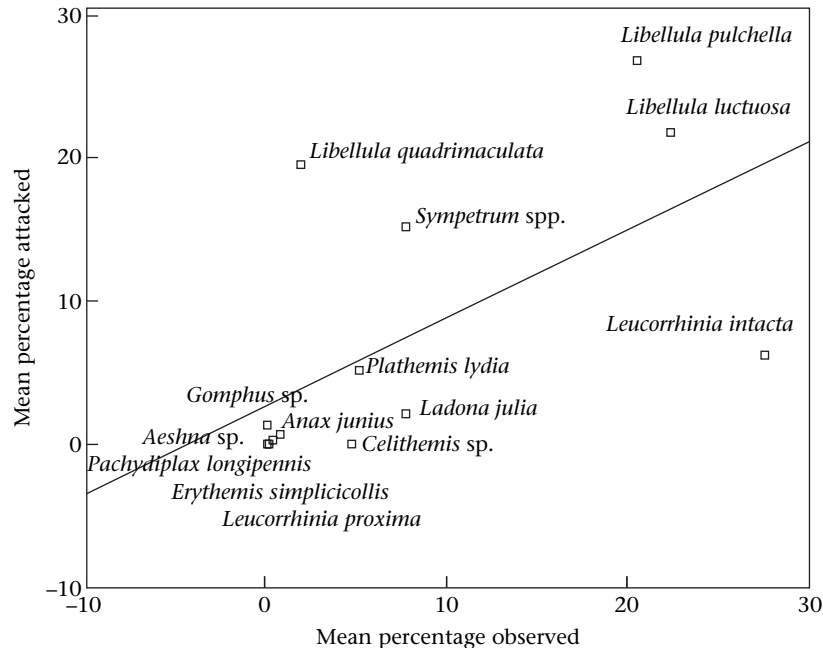


Figure 3. The relation between the arithmetic mean percentage of dragonfly species observed in the experimental field in each survey and the arithmetic mean percentage of attacks made by each of the species over our experiments.

versus black artificial prey, 2003) and 6b (black-and-yellow versus black artificial prey, 2004) separately. Only *Sympetrum* spp. and *Libellula luctuosa* attacked the prey types in experiment 6a and none attacked one prey type over another (2003: $\chi^2_1=0.053$, $P=0.818$; 2004: $\chi^2_1=1.883$, $P=0.17$).

DISCUSSION

Dragonflies were abundant in our test area and were likely to be amongst the most common predators on small aerial insects. The potential prey in our test area (collected in our Malaise-traps) included mimetic and nonmimetic flies as well as a variety of warningly coloured Hymenoptera. Thus, the types of natural prey items presented in our experiments were common at the site during our study, indicating that the dragonflies were likely to have previous experience with these species.

Our first set of experiments (1–3) revealed that dragonflies preferred small flies (Diptera) to large flies. This result is contrary to what one would expect if dragonflies were simply attacking the most detectable prey or seeking the largest potential meal. This preference for smaller prey may be due to ease of prey handling or lower energy costs to the predator in subduing the prey. Since different species of nonmimetic flies were used in this experiment, there could have been a species bias in dragonflies' prey choice; however, using artificial prey, the same results were found. Although this is the first controlled measure of size-based prey preference for adult dragonflies, our results are consistent with earlier observations. Pritchard (1964) examined the guts of 293 dragonflies and reported small Diptera as the largest part of their diet. Corbet

(1999) also listed small flies as a large component of dragonflies' diet. These data support Kauppinen & Mappes's (2003) efforts to control for prey size and may help to explain why they reported so few physical attacks on large flies and wasps in their study, as we also found.

Most importantly, experiments 4–7 showed that there was no tendency for dragonflies to avoid attacking wasp mimetic hover flies or brightly coloured artificial prey. Thus, when we presented the small mimetic hover fly *T. geminatus* together with small flies (*H. rapax*) to dragonflies, our results indicated no significant difference between the number of dragonfly attacks on the two prey types. To control for a possible species effect, we recorded the attack rate of dragonflies on mock-painted versus black-painted hover flies of the same species. Dragonflies did not preferentially attack either of the two prey types. Similarly, dragonflies showed no significant difference between the number of attacks on small black-and-yellow-striped artificial prey and small black-painted artificial prey. These combined data indicate that small mimetic hover flies gain no clear advantage from their yellow-and-black pattern in the context of predation by dragonflies.

One possible argument against presenting prey types experimentally in a pairwise manner is that in nature, predators might not encounter the two prey types in proximity. However, the single-presentation method might be more prone to experimenter bias. We therefore used both single and pairwise presentations in the experiments with artificial prey. The results using both presentation methods showed a significant difference between the number of attacks on large and small artificial prey, regardless of whether the dependent variable was mean time to attack or proportion of prey attacked. We also found no significant difference between the number of

attacks on black-and-yellow artificial prey and the number of attacks on black artificial prey using either the single-presentation method or the pairwise method.

Our failure to reject the null hypothesis of no selectivity in our experiments with wasp-like prey may have resulted from low sample sizes, small effect sizes or both (Thomas & Juanes 1996). With high power (0.8), effect sizes of 70% attacks on one prey species (a 20% departure from the null hypothesis) would be detected after 47 replicates of our pairwise presentations (Minitab version 14, Minitab, State College, Pennsylvania, U.S.A.). Our experiments using mock-painted versus black-painted hover flies, *E. transversa*, and black-and-yellow-painted artificial prey versus black artificial prey both had at least this power, which is considered acceptable for most scientific purposes (Cohen 1988). Of course, these values represent power estimates for the detection of a relatively large effect; a smaller effect would require greater replication to detect with high probability. Some authors have proposed that it is more informative to cite the confidence interval of the difference when summarizing a nonsignificant result, rather than the statistical power per se (Hoenig & Heisey 2001; Colegrave & Ruxton 2003). In our study, the observed difference in the sample means between the two single-presentation treatments, using black-and-yellow versus black artificial prey, was only 0.033, but the 95% confidence limits for this difference (based on the normal approximation to the binomial) were from -0.109 to 0.175 , with a zero effect size occurring in the central portion of the distribution. Although all statistics are based on probabilistic assessments, the most conservative explanation for our results is that dragonflies are relatively undeterred by yellow-and-black markings.

In experiment 8, dragonflies avoided equally mock-painted and black-painted *D. arenaria*. One explanation for this result is that dragonflies might not be active at the time the experiment took place. However, in experiment 9 (*T. geminatus* versus *D. arenaria*), which was conducted at the same time, dragonflies rapidly attacked the hover flies but left the wasps untouched. Although increasing the size of aposematic prey might increase the effect of the warning signal (Gamberale & Tullberg 1996), in our study, dragonflies avoided large prey that were both warningly coloured and not warningly coloured (experiment 8). Thus, prey size and not the black-and-yellow pattern appears to be the main factor prohibiting dragonflies from attack.

It is conceivable that certain species of hover fly are unpalatable to invertebrate predators (i.e. they are aposematic rather than mimetic; Gilbert 2005). However, dragonflies attacked, and spent approximately equal times feeding on hover flies and small flies, which indicates that the hover fly species *T. geminatus* was palatable to dragonflies. Of course, if hover flies were completely free-flying, then they may elicit a different response from predators than if they were tethered. Moreover, dragonflies might also use specific characteristics such as antennae length or general body shape to detect potential prey. Such hypotheses need to be tested, but our results suggest that colour cues themselves do not appear sufficient to inhibit attack.

Either the lack of a UV component or possible odour from the paints could also have biased our results. However, there is no empirical evidence of a UV component in the colour pigments of either wasps or hover flies (Gilbert 2005). Moreover, dragonflies mainly use visual cues to detect their prey, so it is unlikely that the smell of the prey types affected the dragonflies' preference (Corbet 1999).

Although we observed no significant associations between dragonfly size and/or species and their feeding preferences, we were aware of possible seasonal effects during our experiments. For instance, towards the end of the season, dragonflies of the genus *Libellula* (medium-sized dragonfly) declined in numbers and were replaced by *Sympetrum* spp. (small-sized dragonfly). However, each prey-choice experiment was conducted for a relatively short period (maximum duration of 5 days), and the dragonfly community was the same within each experiment, so it is unlikely that seasonal effects could bias our interpretation in any individual experiment. Nevertheless, the possibility of seasonal effects requires caution when comparing preferences between experiments.

Our results suggest that yellow-and-black flies are at no selective advantage compared to black flies in the context of odonate predation, but Kauppinen & Mappes (2003) concluded the opposite. However, the two studies are not necessarily contradictory. Our work focused on smaller flies; we explicitly controlled for encounter, and we considered only the number of actual physical attacks by dragonflies. In contrast, Kauppinen & Mappes investigated the response of dragonflies to larger flies and wasps after encounter, and they considered a much broader suite of response behaviours (not all of which may influence selection on prey coloration). Another potential explanation for the differences between the two studies in the dragonflies' responses towards black-and-yellow prey types might lie in temporal and spatial differences. Under natural environmental conditions, the proportion of predators that find wasps unprofitable may vary in both time and space (Endler & Mappes 2004). The predator species used by Kauppinen & Mappes (2003), *Aeshna grandis*, is a midair forager (Corbet 1999), and it is possible that this species incorporates larger prey items into its diet. Although individuals of the genera *Aeshna* and *Anax* (Aeshnidae) were among the largest dragonflies present in the field during our experiments, these dragonflies made very few attacks. Furthermore, the dragonfly species that attacked the prey types in our experiments were mainly 'perchers' (i.e. sit-and-wait predators that take flight after they have spotted a potential prey). Differences in these predators between studies may therefore account for differences in prey choice.

Our results indicate that, although dragonflies tend to prefer attacking small prey over large prey, they are not inhibited by the yellow-and-black patterns sometimes shown by aposematic and mimetic prey. Although our study suggests that dragonflies may not select for protective coloration in aerial insect prey, we cannot rule out the effect of other insect predators in the evolution of mimetic patterns in invertebrates. Researchers have only begun to address this phenomenon, and there is a need

for more experimental studies of the potential effect of other invertebrate predators in shaping warning signals and mimicry.

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