

Are community patterns in flight height driven by antagonistic interactions?

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Large libellulid dragonflies often fly higher than smaller libellulids. We hypothesized that this size-related pattern in flight height might be caused by aggressive displacement. We tested this hypothesis by using a 30 m “dragonfly zip-line” to reel dead dragonfly decoys of four species of different sizes (*Erythemis simplicicollis*, *Libellula incesta*, *Pachydiplax longipennis*, and *Perithemis tenera*) along a shoreline at four different heights (20, 60, 100, and 140 cm), counting the number of investigations made by large patrolling *Libellula incesta* and *Libellula luctuosa* males. We hypothesized that decoys of smaller species would be investigated and attacked at higher frequency when they were reeled high, in the *Libellula* flight zone, than when they were reeled at their natural low height. This hypothesis was falsified; both *L. incesta* and *L. luctuosa* investigated high-flying decoys significantly less frequently than low-flying decoys. *Perithemis tenera* decoys were investigated less frequently than other decoys by both species, but *L. incesta* investigated *E. simplicicollis*, *P. longipennis*, and *L. incesta* decoys with increasing frequency whereas *L. luctuosa* investigated these three species at equal rates. These patterns correlate with the degree of morphological similarity between patrolling species and decoys, consistent with likely patterns of “mistaken identity” by patrolling *L. incesta* and *L. luctuosa* males. We suggest that patrolling males may preferentially investigate other low-flying males in the hopes of finding a mate-guarded female.

Keywords: dragonfly; *Libellula incesta*; *Libellula luctuosa*; flight behavior; flight height; interspecific interactions; competition; niche partitioning; mistaken identity

Introduction

Aggressive interactions between heterospecific male dragonflies are frequent and easily observed, making odonates model systems for studies in competition and community structure (Corbet, 1999; Suhonen, Rantala, & Honkavaara, 2008; Tynkkynen, Kotiaho, & Svensson, 2008). Although some interactions are best explained as cases of “mistaken identity” by overzealous territorial males (Schultz & Switzer, 2001), persistent interference competition can cause resource partitioning between species (König, 1990; Moore, 1964; Rehfeldt & Hadrys, 1988; Soeffing, 1990; Worthen & Jones, 2006, 2007; Worthen & Patrick, 2004). Some patterns in resource use, like perch height and flight height, correlate with body size; larger species tend to perch higher (Moore, 1991; Warren, 1964; Williams, 1976; Worthen & Jones, 2006, 2007) and fly higher (Perry, Perry & Perry, 1977) than smaller species. Because body size often correlates with competitive ability (Corbet, 1999, p. 337; Moore, 2000; Worthen & Jones, 2007), and coexisting libellulid

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species may vary more than 7-fold in body mass (Worthen & Jones, 2006), asymmetrical competition is an obvious hypothesis for explaining patterns of resource use that correlate with body size.

Perch height patterns are driven by size-dependent competitive hierarchies; larger species displace smaller species from taller perches, relegating smaller species to lower ones (Worthen & Jones, 2006, 2007; Worthen & Patrick, 2004). There are certainly species that contradict this pattern; *Plathemis lydia* (Drury) and *Erythemis simplicicollis* (Say) tend to fly and perch much lower than other species their size, whereas pennants (genus *Celithemis*) tend to perch a bit higher than other species their size (Worthen & Jones, 2007). Nevertheless, the relationship between body size and perch height holds for many libellulid communities (Moore, 1991; Warren, 1964; Williams, 1976; Worthen & Jones, 2006, 2007).

Community patterns in flight height have received far less attention than patterns in perch height. Although flight height is dynamic – changing with abiotic conditions and the presence of prey insects (Iwasaki, Suda, & Watanabe, 2009), predators, conspecific competitors, heterospecific competitors, and potential mates (Martens, 2001) – there are anecdotal reports that flight height also correlates with body size (Corbet, 1999, p. 369; Perry et al., 1977). In the southeastern USA, for example, small species such as *Perithemis tenera* (Say), *Erythrodiplax minuscula* (Rambur), and *Nannothemis bella* (Uhler) fly close to the water; medium-sized *E. simplicicollis* (Say) and *Pachydiplax longipennis* (Burmeister) typically fly less than a meter off the water, while *Libellula incesta* Hagen and *Libellula luctuosa* Burmeister tend to fly more than one meter off the water.

Here we test the simple hypothesis that, like patterns in perch height, flight height is influenced by a size-dependent, antagonistic hierarchy among species. This pattern could result from competition or predation. In either case, we hypothesize that larger species will investigate and attack smaller species at a higher frequency when smaller species are flying high – in the vertical niche of larger species – than when smaller species are flying low in their own vertical niche.

Materials and methods

Study site

The experiment was conducted at Swan Lake on the campus of Furman University in Greenville, SC, USA (latitude/longitude: 34°55'46.15"N, 82°26'28.09"W, elevation 306 m), from 19 June through 2 August 2012. Swan Lake is a 12 ha man-made impoundment, constructed in the late 1950s. Approximately 15% of the perimeter is naturally vegetated; the remaining shoreline is turf grasses. The summer odonate community is dominated by *Erythemis simplicicollis* (Say), *Libellula incesta*, *L. luctuosa*, *Pachydiplax longipennis*, and *Perithemis tenera*. *Celithemis elisa* (Hagen), *C. eponina* (Drury), and *C. fasciata* Kirby are also common.

Protocols

Four common species, representing a five-fold difference in size, were selected as decoys: (mean mass, Worthen and Jones, 2006): *P. tenera* (67.7 mg), *P. longipennis* (196.3 mg), *E. simplicicollis* (214.9 mg), and *L. incesta* (395.5 mg). We measured responses of two common large species, *L. incesta* and *L. luctuosa*, to discriminate species-specific responses from those related to body size. Males of the decoy species were collected periodically by net, killed with ethyl acetate, and preserved in acetone with wings outstretched horizontally in flying position. These decoys were reeled along the shoreline on a 30 m “dragonfly zip-line” constructed of extension cord reels (Bayco), reinforcing bar (“re-bar”), and 0.3 mm monofilament fishing line (Figure 1). The reels were modified by adding wooden dowels as “cross spars” between the flanges, approximately

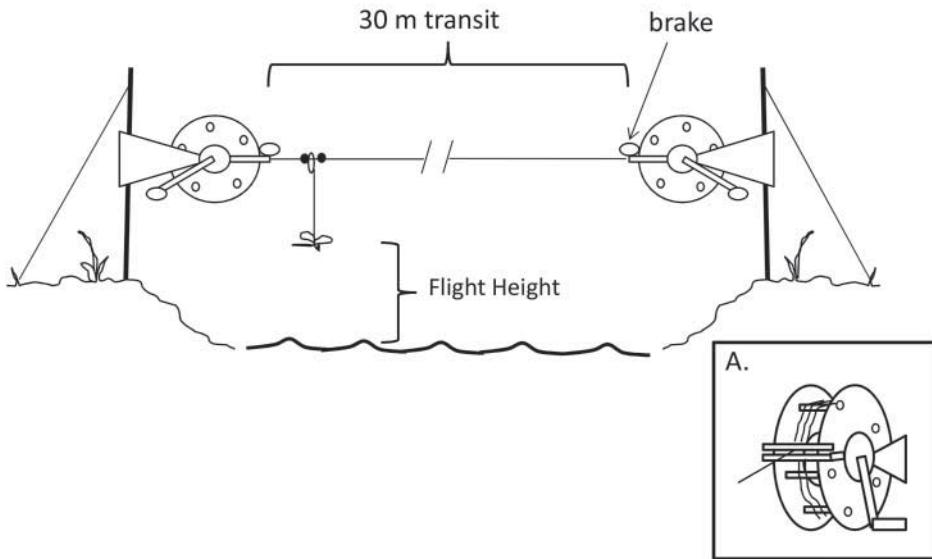


Figure 1. Dragonfly “zip-line” used for reeling decoys along the shore at different heights. The reels were placed 30 m apart, and were raised and lowered on the rebar supports. The “brake” created drag to keep the monofilament line taut and reduce bouncing during transit; it was removed from the gathering reel during reeling. Cross spars were added between the flanges of each reel to increase the functional circumference of the drum and increase transit speed (approximately 1 m s^{-1}).

3 cm from the outer edges, to increase the functional circumference of the spool (Figure 1A). A gentle reeling speed gathered approximately 1 m of line per second. Holes were drilled in the reel supports to accommodate a shaft of re-bar. The reel was raised and lowered on the re-bar shaft to change the height of the zip-line; a screw clamp was placed on the shaft, below the reel, as a stop. The line left the reel over the reel handle, which was sheathed in aluminum flashing to prevent the line from cutting grooves in the soft plastic. A 10 cm piece of PVC tubing was anchored to the handle with a short bungee-cord; this acted as a “drag” when line was spooled off the reel, creating enough resistance to maintain a taut line and a smooth transit.

A decoy was suspended on a 20 cm “leash” of 0.3 mm monofilament fishing line (Figure 1). A hole was made through the decoy’s thorax (dorsal to ventral) with a thin wire. One end of the leash was threaded through the hole, and a small “split-shot sinker” (fishing weight) was clamped to the line below the decoy (Figure 1). The decoy rested on the sinker, and the sinker gave the leash and decoy enough mass to complete transits smoothly in light breezes. A small paper clip was tied to the other end of the leash. The paper clip was looped over the monofilament “zip-line”, between two small split-shot sinkers clamped to the zip-line as stops (Figure 2). As the decoy was reeled along the transit, the number and species of interactions by patrolling dragonflies were recorded. Interactions were scored as “investigations” if the patrolling dragonfly hovered for at least 1 s while facing the decoy within a ~ 30 cm radius. Interactions were scored as “attacks” if the patrolling dragonfly touched the decoy with its legs. All attacks were also scored as investigations. After completing a transit, the leash was unhooked from the zip-line, rotated 180° , and repositioned between the two sinker stops with the dragonfly pointing back down the transect. The drag was applied and the dragonfly was reeled down the transit from the other end. A decoy was run for 10 consecutive transits, at approximately 10 minute intervals. Decoys were replaced *ad libitum*, when they became damaged or worn.

Over 100 transits were also run with live decoys lassoed behind the forewings. These decoys would flap spasmodically during a transit, hang at awkward angles, and attack investigating

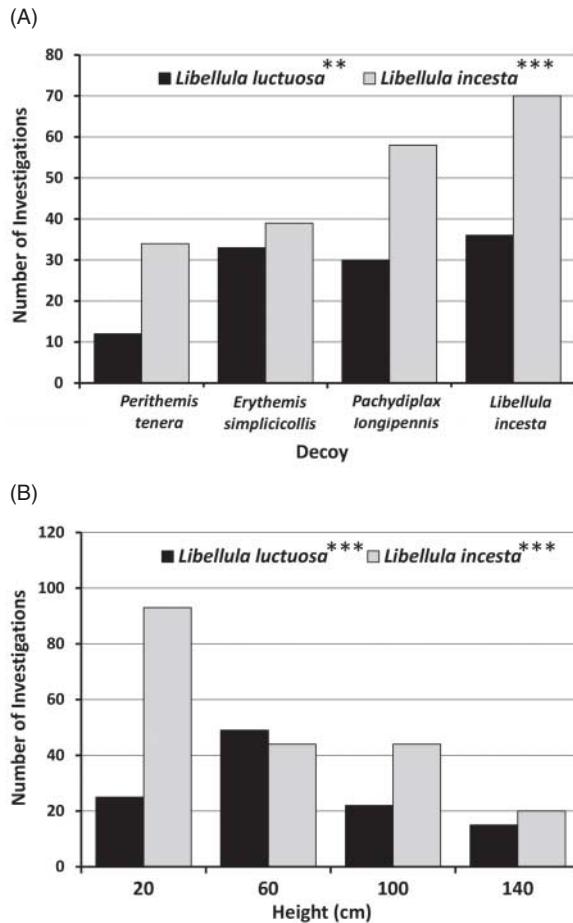


Figure 2. The number of direct investigations of moving decoys made by patrolling male *Libellula luctuosa* ($n = 111$) and *Libellula incesta* ($n = 201$), as functions of (A) decoy species and (B) decoy flight height. Both patrolling species exhibited statistically significant differences in investigation frequencies across both decoy species and decoy flight height (see Table 1).

dragonflies. The behavior of these live decoys was less “life-like”, in many respects, than the free glide of a dead decoy. In addition, these behaviors introduced several confounding variables that complicated interpretations of patroller behavior. Consequently, we chose to eliminate the effects of decoy behavior by using only dead decoys, and focus on the effects of flight height.

Experimental design and statistical analyses

Each decoy species was used in 240 total transits, with 60 transits at each of four heights above the water surface: 20, 60, 100, and 140 cm. At each height, 30 transits were run in the morning (within 2 h before solar noon) and in the afternoon (within 2 h after solar noon). Species and height were changed haphazardly after a set of 10 transits was completed. To account for the possibility that patrolling dragonflies were simply investigating a moving object, we also ran a complete series of 240 control transits using a thin 5 cm stick as the “decoy”. These control trials were haphazardly interspersed with the decoy runs, also with 30 transits in the morning and afternoon at each height.

The apparatus was positioned at the same point on the lake for every sampling period. As a result, investigations and attacks were probably not independent of one another, either within a sampling period or between sampling periods on consecutive days, as single patrolling dragonflies were probably scored more than once (pseudoreplication). And, although runs were 10 minutes apart and although decoys were running transits among live flying dragonflies, it is possible that patrolling *L. incesta* and *L. luctuosa* learned to discriminate decoys and altered their behavior. However, given the high density of patrolling *L. luctuosa* and *L. incesta*, their long patrol sorties, their short lives and transient territorial ownership, and the need to investigate a decoy to discriminate it, we believe these effects were probably small and were minimized by sampling across several months.

The direct and interactive effects of patrolling species, decoy species, and decoy flight height on the frequency of investigations made by patrolling *Libellula incesta* and *L. luctuosa* dragonflies were assessed with hierarchical log-linear analyses (IBM, 2010). For effects that were statistical significant in log-linear analyses, treatments were compared with chi-square goodness-of-fit tests. We hypothesized that investigations by both large patrolling species should be an interactive function of decoy size and decoy flight height, with investigations increasing as decoy flight height increased and decoy size decreased. In sum, these comparisons tested the hypothesis that aggressive interactions by large species – either competitive or predatory – exclude small species from high flight heights and restrict them to lower flight/activity niches.

Results

Libellula incesta and *Libellula luctuosa* readily investigated moving decoys, examining them 201 and 111 times, respectively, in a total of 960 decoy transits. On several of these occasions they physically attacked the decoys by touching them with their tarsi (11 and five times, respectively), but there were no incidences of predation in our experiment. In contrast, they investigated the “control sticks” only five and four times, respectively; significantly less frequently than the least-investigated decoys (*L. luctuosa*: control versus *P. tenera* decoys, $\chi^2 = 4.0$, $df = 1$, $p < 0.05$; *L. incesta*: control versus *P. tenera* decoys, $\chi^2 = 21.56$, $df = 1$, $p < 0.001$). Having determined that *L. luctuosa* and *L. incesta* differentiate moving dragonfly decoys from moving sticks, we limited subsequent statistical analyses to investigations of decoys only.

The frequencies of investigations varied significantly as functions of the direct and interactive effects of patrolling species, decoy species, and decoy flight height (Table 1a). When analyzed separately, investigations by both patrolling species were significantly affected by the direct and interactive effects of decoy species and decoy flight height (Table 1b, c, Figure 2). *Libellula incesta* investigated decoys 211 times, significantly more frequently than *L. luctuosa* (111 times, “Species” effect, Table 1a; Figure 2A), probably because of their greater abundance.

Table 1. Hierarchical log-linear analyses describing differences in the frequency of investigations by *Libellula incesta* and *Libellula luctuosa* of four decoy species flown at four different heights.

Effect	a. Both species			b. <i>Libellula incesta</i>			c. <i>Libellula luctuosa</i>		
	df	Partial χ^2	p	df	Partial χ^2	p	df	Partial χ^2	p
Species	1	30.223	0.001	—	—	—	—	—	—
Decoy	3	26.610	0.001	3	15.256	0.002	3	19.947	0.001
Height	3	55.577	0.001	3	50.761	0.001	3	27.783	0.001
Decoy \times Height	9	25.910	0.002	9	17.87	0.037	9	16.64	0.055
Species \times Decoy	3	10.120	0.018	—	—	—	—	—	—
Species \times Height	3	24.504	0.001	—	—	—	—	—	—
Species \times Decoy \times Height	9	8.600	0.475	—	—	—	—	—	—

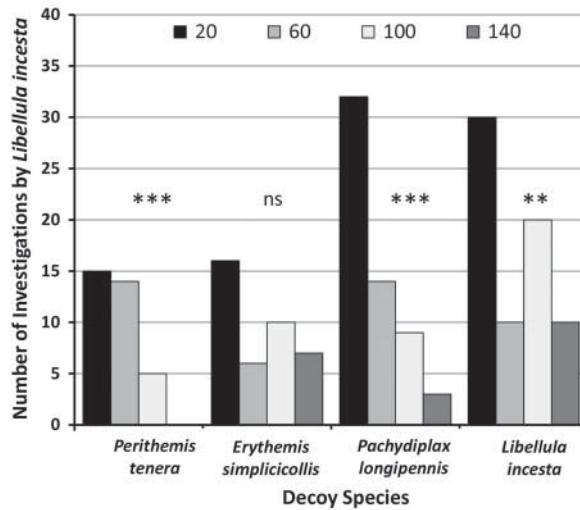


Figure 3. The number of direct investigations made by patrolling male *Libellula incesta* ($n = 201$) of different decoy species at different flight heights. The frequency which *Libellula incesta* investigated decoys depended on the flight height for *P. tenera* ($n = 34$), *P. longipennis* ($n = 58$), and *L. incesta* ($n = 70$) decoys, but not for *E. simplicicollis* ($n = 39$; chi-square tests of independence, $**p < 0.01$, $***p < 0.001$, $ns = p > 0.05$).

What is more important, however, and is unrelated to difference in abundance, is that the two patrolling species investigated decoys in significantly different patterns (“Species \times Decoy” effect, Table 1a; Figure 2A). *Libellula luctuosa* investigated *P. tenera* decoys less frequently than decoys of the other species, which were investigated at roughly the same rate (“Decoy” effect, Table 1b; Figure 2A). *Libellula incesta* also exhibited less interest in *P. tenera*, but progressively more interest in *E. simplicicollis* and *P. longipennis*, and the most interest in conspecific decoys (“Decoy” effect, Table 1c; Figure 2A). *Libellula luctuosa* and *L. incesta* also differed in their pattern of investigations across decoy flight heights (“Species \times Height” effect, Table 1a; Figure 2B). *Libellula luctuosa* investigated decoys flying at 60 cm more frequently than decoys at other heights (“Height” effect, Table 1c; Figure 2B), whereas *L. incesta* investigated decoys flying at 20 cm most, with declining interest as decoy flight height increased (“Height” effect, Table 1b; Figure 2B).

For *L. incesta*, the effect of decoy flight height on the frequency of investigation varied across decoy species (“Decoy \times Height” effect, Table 1c; Figure 3). *Perithemis tenera* decoys were investigated by *L. incesta* at equal rates at 20 and 60 cm, but were ignored at 140 cm ($\chi^2 = 18.47$, $df = 3$, $p < 0.001$; Figure 3). In contrast, *L. incesta* investigated *E. simplicicollis* decoys at all heights at roughly equal frequencies ($\chi^2 = 6.02$, $df = 3$, $p > 0.10$; Figure 3). *Pachydiplax longipennis* decoys were often investigated by *L. incesta* at low flight heights, with significantly decreasing interest as flight height increased ($\chi^2 = 32.34$, $df = 3$, $p < 0.001$; Figure 3). And, although *L. incesta* also investigated conspecific decoys most often when they were flown low ($\chi^2 = 15.71$, $df = 3$, $p < 0.01$), conspecific decoys were consistently investigated at higher flight heights as well (Figure 3).

For *L. luctuosa*, the effect of decoy flight height on the frequency of investigations also varied across decoy species, to a marginally significant degree (“Decoy \times Height” effect, Table 1b; Figure 4). *Erythemis simplicicollis* were investigated by *L. luctuosa* more at intermediate heights than when flown high or low ($\chi^2 = 8.82$, $df = 3$, $p < 0.01$; Figure 4), whereas *L. luctuosa* investigated *P. longipennis* decoys most at the two lowest flight heights ($\chi^2 = 18.80$, $df = 3$, $p < 0.001$; Figure 4). *Libellula incesta* decoys were investigated at all heights at roughly the same rate ($\chi^2 = 7.33$, $df = 3$, $p > 0.05$; Figure 4). *Perithemis tenera* decoys were not investigated

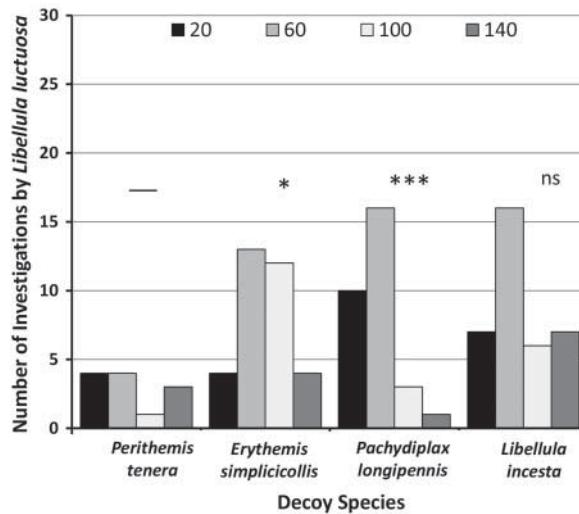


Figure 4. The number of direct investigations made by patrolling male *Libellula luctuosa* ($n = 111$) of different decoy species at different flight heights. The frequency which *Libellula luctuosa* investigated decoys depended on the flight height for *E. simplicicollis* ($n = 33$) and *P. longipennis* ($n = 30$) decoys, but not for *L. incesta* ($n = 36$; chi-square tests of independence, * $p < 0.05$, *** $p < 0.001$, ns = $p > 0.05$). There were insufficient data for *P. tenera*, $n = 12$).

frequently enough by *L. luctuosa* to compare the frequency of investigations at different heights (expected values < 5).

Discussion

The goal of this experiment was to test the hypothesis that the observed correlation between dragonfly flight height and body size results from hierarchical size-dependent antagonistic relationships. We predicted that large *L. incesta* and *L. luctuosa* males would investigate and attack smaller species at a higher frequency when smaller species were flying high – in the vertical niche of these larger species – than when smaller species were flying low. This hypothesis was falsified for both large species. *Libellula incesta* and *L. luctuosa* males investigated decoys of three smaller species (*Erythemis simplicicollis*, *Pachydiplax longipennis*, and *Perithemis tenera*) at higher rates when the decoys were flown low than when the decoys were flown high; in four of six cases this was statistically significant. This pattern also held for investigations of *L. incesta* decoys, although only to a statistically significant degree by patrolling *L. incesta* males. So, although there were species-specific responses to different decoy species by both *L. incesta* and *L. luctuosa*, the overriding pattern was that patrolling *L. incesta* and *L. luctuosa* males investigated low flying decoys significantly more frequently than they investigated high-flying decoys.

Libellula incesta and *L. luctuosa* differed in patrolling behavior; *L. incesta* investigated decoys flown at 20 cm the most, with decreasing interest as decoy flight height increased. This pattern was most pronounced for *L. incesta* investigating *P. tenera* and *P. longipennis* decoys; *L. incesta* maintained some interest in *E. simplicicollis* and *L. incesta* decoys when they were flown high (though still less than when they were flown at 20 cm). *Libellula luctuosa* showed little interest in *P. tenera* at any height, and the most interest in *E. simplicicollis*, *P. longipennis*, and *L. incesta* at intermediate heights. Again, however, neither *L. incesta* nor *L. luctuosa* showed a preference for investigating or attacking high-flying decoys of these three smaller species.

These same species show hierarchical, size-dependent competition for perches, with larger species displacing smaller species from tall perches, relegating small species to low perches unused by larger species (Worthen & Jones, 2006, 2007). The difference between patrolling behavior and competition for perches might be due to the context and correlates of the different stimuli. A tall perch provides an ideal view of a local territory, and large size gives some species a competitive advantage for acquiring and holding these resources. Interspecific aggression is explainable in this context, because of the fitness advantage to all males that can hold a tall, high-quality perch. Driving off a conspecific from a perch provides the additional fitness benefit of increasing the likelihood that the winner mates within that territory, or can usurp the territory from a dominant male as it patrols (Córdoba-Aguilar, 1994; Eberhard, 1986). However, the value of a perch varies between species. *L. luctuosa* males employ two reproductive strategies; subordinate males perch while dominant territorial males patrol (Moore, 1987, 1989).

Flying males, however, might provide different information than perching males. A low-flying male, particularly of a high-flying species, might be mate-guarding an ovipositing female. *Libellula luctuosa* males often mate-guard about 20 cm above the female (Campanella, 1975) and about 30–40 cm above the water – coinciding with the height at which patrolling males showed the greatest interest in decoys in this study. Investigating low flying males may have a significant fitness benefit by providing a patrolling male with an opportunity to mate. The benefits might even be large enough to compensate for the energetic costs of investigating morphologically similar heterospecifics, even if the investigations are ultimately cases of “mistaken identity” (Schultz & Switzer, 2001).

The patterns of investigation by *L. luctuosa* and *L. incesta* are generally consistent with this hypothesis. *Libellula incesta* males have clear wings and a dark, slate-blue colored thorax and abdomen. *Libellula luctuosa* also has a slate-blue body, but is 5% larger (in wingspan and length) and has wings that are completely dark in the proximal half. Both of these large dark species showed the least interest in *P. tenera*, a small, orange-bodied, orange-winged species that is more easily confused with wasps than with *L. incesta* or *L. luctuosa*. Males of *E. simplicicollis* and *P. longipennis* are only about 3/4 the size (in wingspan) of the *Libellula* species; *E. simplicicollis* males have a light-blue body and *P. longipennis* males have a slate-blue abdomen. Both species lack the black basal wings of *L. luctuosa*, and so are somewhat more similar in size and coloration to *L. incesta*. Patrolling *Libellula incesta* males showed little interest in *P. tenera*, more interest in *E. simplicicollis* and *P. longipennis*, and the most interest in conspecifics, consistent with the “mistaken identity” hypothesis (Schultz & Switzer, 2001). Investigations by *L. luctuosa* can also be interpreted in this light. The orange *P. tenera* were largely ignored, and the blue species – all equally distinguishable from *L. luctuosa* by clear wings, were investigated at roughly the same low rate.

Intraspecific aggression among males is usually explained as a mechanism to acquire or defend a mate or territory (Corbet, 1999; Suhonen et al., 2008). There is obvious selective value, in terms of relative fitness, of winning a mate while also reducing the mating success of other conspecific males (Baird & May, 2003). Success in intraspecific interactions often goes to the younger combatant, or the one with greater fat reserves or immunocompetence (Suhonen et al., 2008).

Interspecific aggression is also common, but it is more difficult to explain in terms of improved mating success. Spending time and energy to drive off heterospecific males could increase the probability of mating if females prefer areas with less overall dragonfly activity or lower overall dragonfly abundance, or if aggressors are more likely to retain a territory. Other fitness benefits are also possible, because additional species in a territory might interfere with feeding, mating, or oviposition, attract predators, or increase the density of dragonfly larvae that might compete with or consume offspring or attract larger density-dependent predators.

But because these scenarios are all related to reducing overall adult or larval abundance, males should drive off intruders of all species with equal zeal. This is rarely the case, however. Territorial males are more likely to attack intruders that are similar in size, coloration, or wing pattern, suggesting that males may be mistaking interspecific intruders for conspecifics.

Intraguild predation is also a mechanism that could produce vertical niche partitioning. Small species may gain some protection from larger predatory species by flying close to the water. Our experiment, however, also refutes this hypothesis. First, decoys were never preyed on, and we never observed a predation event among dragonflies in the area. Second, small species were approached less frequently when they were flying high and, presumably, more vulnerable to predation.

In conclusion, flight heights of *E. simplicicollis*, *L. incesta*, *P. longipennis*, and *P. tenera* are not constrained by interspecific encounters with larger, higher-flying species. Contrary to predictions of the antagonism hypothesis, decoys were investigated more when they were flying low than when they were sharing the vertical niche of the patrolling species. We suggest that patrolling males might preferentially investigate other low-flying dragonflies that could indicate the presence of an ovipositing female. In addition, patrolling *L. incesta* and *L. luctuosa* investigated decoys in a pattern correlating with their morphological similarity to the patrolling species, consistent with “mistaking the identity” of heterospecifics during a search for potential mates (Schultz & Switzer, 2001).

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