

Competitive interactions affect perch-height preferences of three Odonata taxa (Coenagrionidae, Libellulidae)

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ABSTRACT

Co-occurring odonate species often perch at different heights. We studied the effects of interspecific and intraspecific interactions on perch-height selection by *Perithemis tenera*, *Pachydiplax longipennis*, and *Enallagma* spp. by creating artificial perch stations and comparing perch selection when species perched alone or together. We also compared the frequency of perch-height use in the presence or absence of *P. tenera* and *P. longipennis* decoys (dead mounted specimens). When species perched alone, *Enallagma* spp. preferred low perches, *P. tenera* intermediate perches, and *P. longipennis* tall perches. This correlated with body mass; larger species used taller perches. Intraspecific responses to decoys were species specific; *P. tenera* showed an aggressive positive response to the presence of a conspecific decoy, whereas *P. longipennis* avoided conspecific decoys by shifting to lower perches. Interspecific effects were more consistent. The presence of living or decoy *P. tenera* at a station caused *Enallagma* to shift to lower perches. Likewise, the presence of living or decoy *P. longipennis* at a station caused *P. tenera* to shift to lower perches. Reciprocal effects were insignificant. These interactions were defined as interference competition because, in the decoy trials, perch-height shifts occurred although all four perches were available to visitors. We conclude that asymmetrical competition contributes to perch-height selection among these species.

INTRODUCTION

Odonata use perches to access prey (May 1984; Eberhard 1986; Gorb 1994; Baird & May 1997), to access mates and oviposition sites (Moore 1952; Ottolenghi 1987; Gorb 1995), to conserve energy (May 1984; Baird & May 1997), and to thermoregulate (May 1976, 1978). Because food, mates, oviposition sites, and sunflecks are often patchily distributed in space and time, high quality perches can be a limiting resource. Competitive interactions for high quality perch sites can be energetically demanding and physically dangerous. For many species, however, the energetic costs of defending a territorial perch are outweighed by the direct and indirect benefits to reproductive success gained by acquiring a mate, an oviposition site, or food (Parr 1983; Wolf et al. 1997; Switzer 2002).

Most overtly aggressive competitive interactions for perch sites occur between conspecifics (Lutz & Pittman 1970; Moore 1987; Schultz & Switzer 2001). These interactions are affected by a complex array of factors, including perception of intruders (Switzer & Eason 2000), priority effects and mating success at a perch (Switzer 2002), site quality (Wolf et al. 1997), posture and perch height (Gorb 1994), site fidelity (Alcock 1989), and the behavioral context of the interaction (Moore 1987). In response to these competitive interactions, some species partition perches based on perch height, with large reproductive males displacing pre-reproductives from preferred perches (Eberhard 1986; Cordoba-Aquilar 1994; Kasuya et al. 1997; Switzer 1997). However, the size effect is often weak, and other variables such as site quality (Eberhard 1987; Cordoba-Aquilar 1994), resident or intruder status (Kasuya et al. 1997), time of arrival (Kasuya et al. 1997) or site tenure (Switzer 2002) can complicate simple size-dependent relationships. Also, it is important to appreciate that taller perches are not always preferred; in *Hetaerina macropus* Selys, reproductive males preferred lower perches than either females or pre-reproductive males (Eberhard 1986).

In many odonate assemblages, there are also obvious interspecific differences in habitat selection. Temporal partitioning occurs when species are active at different times of the day; perhaps as a consequence of differences in thermoregulatory strategies correlating with differences in body size, flight behavior, or coloration (Heinrich & Casey 1978; Samways et al. 1996; DeMarco & Resende 2002). Spatial separation occurs where species perch at different heights or use different substrates for perching or oviposition (Bick & Bick 1972; König 1990; Soeffing 1990; Osborn & Samways 1996; Raab et al. 1996; Reinhardt 1999). Although resource partitioning among odonates is often attributed to the “ghost of competition past” (Connell 1980), aggressive interactions between species have been documented (Moore 1991) and can lead to resource partitioning of perch height (Rehfeldt & Hadrys 1988). There is some suggestion that these interactions might structure communities in a very regular, hierarchical pattern; with small, competitively subordinate species being displaced to shorter perches (Warren 1964; Corbet 1999: 337).

If interspecific competition structures perch selection in odonates, we might expect these interactions to be most obvious among common, aggressive species. In the eastern United States, two of the most common anisopterans of ponds and slow moving streams are *Perithemis tenera* (Say) and *Pachydiplax longipennis* (Burmeister). *P. tenera* is a small species (25 mm maximum body length; Dunkle 1989), but males aggressively defend their perches from conspecifics, flies, butterflies, and other odonates (Bick & Bick 1963; Schultz & Switzer 2001). Males prefer low perches that are further from shore than their oviposition site (Switzer & Walters 2001). This might allow males to watch the oviposition site while detecting intruders or females flying along the shoreline (Switzer & Eason 2000). Males defend one territory per day and, if they mate at that site, will usually return to that vicinity the following day (Switzer 1997a, 1997b). They will also drive small zygopterans like *Enallagma civile* (Hagen) from their vicinity (Bick & Bick 1963). *P. longipennis* is a larger species (44 mm maximum body length; Dunkle 1989) that

prefers taller perches. It is also strongly territorial (Johnson 1962; Robey 1975), and it maintains a short-term fidelity to perch sites (Baird & May 1997; May & Baird 2002). Our objectives were to document patterns of perch-height use by *Enallagma* spp., *P. tenera*, and *P. longipennis*, and to determine whether perch selection is affected by intraspecific and interspecific interactions.

MATERIALS AND METHODS

Experimental design

The perching behavior of *Enallagma* spp., *Perithemis tenera* and *Pachydiplax longipennis* was observed on 12 sampling days between 10 June - 12 July 2003, at a 12 ha man-made lake on the campus of Furman University in Greenville, SC, USA (34°56'N, 82°26'W). The lake was a shallow, highly eutrophic system surrounded by lawns and walking trails. It contained largemouth bass (*Micropterus salmoides*), two large introduced carp (*Cyprinus* sp.), and a resident population of geese and ducks. In summer 2003, the odonate community was dominated by *P. tenera*, a small species that may benefit from competitive release when fish prey on larger odonate larvae (Morin 1984). *P. longipennis* was also abundant even though fish were present; possibly because these larvae become less active in the presence of fish predators (Hopper 2001). The odonate community also contained large populations of species typical of ponds in the Carolinas: *Enallagma civile*, *E. traviatum* Selys, *Erythemis simplicicollis* (Say), *Libellula incesta* Hagen, *L. luctuosa* Burmeister, and *Plathemis lydia* (Drury).

Three sampling areas were established along the western shore of the lake. This shoreline was vegetated to the waterline, had small patches of emergent vegetation, and was the least disturbed region of the lake. Each sampling area was 100 m in length, and was separated from the other sampling areas by at least 50 m. On each sampling day (trial), one area was selected for use. Sampling stations were established every 10 m along the shoreline within the area. At each station, four artificial perches were created by inserting four wooden dowels (7.5 mm diameter) into the sediment so that they protruded above the water level at heights of 3, 12, 21, and 30 cm. The perches were positioned 10 cm apart, 50 cm from shore, and the order of perch heights at a station was randomized. There were 12 trials (separate sampling days) in this experiment. Six trials were conducted in the morning (09:30 - 11:30 h) and six were conducted in the afternoon (14:30 - 16:30 h). These local times were US Eastern Daylight Savings Times (EDT). Sunrise and solar noon were 6:14 EDT and 1:28 EDT on June 10, and 6:24 EDT and 1:34 EDT on July 12, respectively. So, morning trials began approximately four hours before solar noon, and afternoon trials began approximately one hour after solar noon.

We measured the effect of inter- and intraspecific interactions on perch selection by comparing perch selection in the presence and absence of 'decoys' (dead mounted male specimens), and in the presence and absence of live competitors. In each trial, a decoy was placed at five randomly-selected stations. *P. tenera* decoys were randomly assigned to six trials and *P. longipennis* decoys were used in the other six

trials. Each species was used in three morning trials and in three afternoon trials to account for any shifts in diurnal activity. The decoys were anesthetized and killed with ethyl acetate, and placed in an acetone bath for 24 hours. They were glued to wire stakes, and the stakes were positioned 10 cm behind particular perches. In preliminary trials, *P. tenera* preferred 12 cm perches and *P. longipennis* preferred 30 cm perches. So, *P. tenera* decoys were positioned 10 cm behind 12 cm perches and *P. longipennis* decoys were positioned 10 cm behind 30 cm perches in order to mimic typical perch use by these species. In this way, all four perches at each station were available to visiting odonates. Competitive interactions were described by comparing perch use in the presence of decoys with perch use in the absence of decoys. In addition, using data from the 'decoy absent' stations, we measured competitive by comparing perch use when other living odonates were present or absent within an array.

After the perches and decoys were positioned, we began a 2-h observation period. One of us sat 10 m 'inland' from the third station and observed perching activity at stations 1-5 while the other person sat 10 m inland from station 8 and observed stations 6-10. With the use of binoculars, all visiting anisopterans could be clearly distinguished to species. Zygoptera were difficult to discriminate from this distance, but all appeared to be *Enallagma* species. To confirm these identifications, a few specimens were collected at the end of the sampling periods. All collected individuals were either *E. civile* or *E. traviatum*. Each observer recorded as many landings and departures as possible within the 2-h period, noting the species and perch height. Noting departures was critical, because individuals would frequently return to the same perch after driving off an intruder. The only way to know whether a new perch event had occurred was to note the intervening departure. Over the 12 trials we recorded a total of 3,949 perch events.

Comparisons and data analyses

Our first objective was to determine whether taxa preferred particular perch heights. Data from 'decoy absent' stations were pooled across the trials and stations. For each taxon, the data set was further restricted to perch events where that taxon perched alone within a station. χ^2 goodness-of-fit tests were used to determine whether each taxon, when alone, used the perch heights with equal frequency.

We used χ^2 contingency tests to determine whether perch selection by each taxon was affected by the presence of *P. tenera* or *P. longipennis* decoys. Data were pooled across the six trials in which a particular decoy species was used, and perch height use was compared between stations with and without decoys for each taxon. Data were also pooled across stations within each decoy treatment. Again, data sets were limited to perch events where individuals perched alone within a station.

Finally, we used χ^2 goodness-of-fit tests to describe the effect of interference competition by living *Enallagma*, *P. tenera*, and *P. longipennis* visitors on perch site selection by each taxon. For these comparisons, all 'decoy absent' stations were pooled across the trials and stations. However, we could not simply compare the distribution of perch sites used alone with perches used when living interspecifics were present. Because these live odonate visitors were occupying a perch, the

availability of perch sites varied between these two treatments. For instance, *Enallagma* would use 12 cm perches less frequently in the presence of *P. tenera* than when they were alone. However, this was in part because 12 cm perches were often occupied by *P. tenera* and were unavailable to *Enallagma*. So, the expected null model had to correct for the occasions when both species would attempt to use the same perch. With no interference competition, this could be estimated as the product of their independent probabilities of using that perch height (estimated by the frequency of perch site use when alone). So, we estimated the frequency that species A should use perch 1 in the presence of species B as:

$$\text{Species A, estimated frequency at Perch 1} = A_1 = n [p_{1A} - ((p_{1A})(p_{1B}))],$$

where n = number of observed co-occurrences, p_{1A} = proportion of perches at perch 1 by species A when alone, and p_{1B} = proportion of perches at perch 1 by species B when alone. In short, in the absence of interference competition, the estimated perch use should be the frequency of perch use when alone minus the instances where that perch would be sought by the target species but would be occupied by the second species (the product of their independent frequencies of perch use). This computation was repeated for each perch height, generating four estimated frequencies of perch use for species A in the presence of species B. These estimated frequencies no longer summed to n , the number of observed co-occurrences. The frequencies were rescaled to n to determine the expected frequencies of perch height use in the presence of another species. The observed and expected values were compared with a χ^2 goodness-of-fit test.

In summary, we described: (1) the pattern of perch site use by each species when alone; (2) the effect of *P. tenera* and *P. longipennis* decoys on perch site selection by each species; and (3) the effect of living interspecific competitors on perch site selection by each species. For all analyses, by pooling between trials, between stations, and within stations, each perch event was considered to be a separate, independent observation. Obviously, for territorial species such as these, we were surely resampling single individuals that were returning to the same perch or station after defensive forays or foraging flights. This violates the assumption of independence implicit in statistical tests. And, these individual differences can be meaningful. For instance, Switzer (2002) demonstrated that *P. tenera* males vary in the length of territorial tenure (how long they defend a site). So, within a station, an individual may return to the same perch for individual preference (not 'species' preference), and return to that perch over an individually variable interval. We did not mark individuals, and we did nothing that could correct or compensate for the effects of individual differences affecting our results at this scale. However, by distributing our sampling across a large area and across several weeks, we maximized the number of individuals in our sample and reduced the impact of any anomalous individuals. For instance, by simultaneously recording perching at 10 stations separated by 10 m, we were certainly observing the behavior of at least 10 *P. tenera* and *P. longipennis* on any given day, because these species appear to have much smaller territories (Switzer & Walters 1999; May & Baird 2002). And, because no stations were sampled on consecutive days and most areas were sampled only once

per week, it is also unlikely that *P. tenera* males were resampled; most *P. tenera* defend territories for less than one week (Switzer 2002). *P. longipennis* may be more long-lived and problematic, but recapture rates over several weeks range from 10-50% (Baird & May 2002). Finally, by randomly assigning treatment groups to stations and by randomizing perch order within stations, the effects of individual preferences should be randomized across these variables. So, we acknowledge that individual differences may confound these patterns, but we designed the experiment to attempt to average over these effects at larger scales (Oksanen 2001).

RESULTS

Perch selection by *Enallagma* spp.

When perching alone, *Enallagma* individuals exhibited a significant preference for low perches, using the 3 cm perches 51.0% of the time (Table 1A; 'decoy absent' stations, pooled across trials and stations). *Enallagma* used higher perches significantly more frequently in the afternoon than in the morning trials ($\chi^2 = 10.39$, $df = 3$, $p < 0.05$), but were equally active during these periods (161 perches in morning, 188 in afternoon; $\chi^2 = 2.06$, $p = \text{n.s.}$). When a single living *Perithemis tenera* was also perched at a station, *Enallagma* displayed a significant perch-height shift and used low perches with even greater frequency than expected by the random co-occurrence model (67.0%, Table 1A). This interspecific competitive effect was confirmed by the decoy studies. *Enallagma* used lower perches at significantly higher frequencies in stations with *P. tenera* decoys than in stations without *P. tenera* decoys (Table 1A). In addition, *Enallagma* used stations with *P. tenera* decoys significantly less often ($n = 102$) than stations without *P. tenera* decoys ($n = 141$; $\chi^2 = 6.26$, $df = 1$, $p < 0.05$).

The presence of a *Pachydiplax longipennis* decoy had the opposite effect. *Enallagma* used higher perches in the presence of *P. longipennis* decoys than they used at stations where *P. longipennis* decoys were absent (Table 1A). Although they move towards *P. longipennis* decoys within a decoy station, *Enallagma* used stations with *P. longipennis* decoys at a significantly lower frequency ($n = 127$) than stations without these decoys ($n = 208$; $\chi^2 = 19.59$, $df = 1$, $p < 0.0001$). The presence of a live *P. longipennis* elicited the same upward shift in *Enallagma* perch use, but not to a statistically significant degree (Table 1A).

Perch selection by *Perithemis tenera*

When males perched alone at a station, they preferred perches of intermediate height and used the 12 cm perch for 51.1% of their perch events (Table 1B; 'decoy absent' stations pooled across trials and stations). There was no difference in perch site distribution between morning and afternoon trials ($\chi^2 = 1.41$, $df = 3$, n.s.), but *P. tenera* were more active in morning trials (534 perches in morning, 462 in afternoon; $\chi^2 = 5.60$, $p < 0.05$). The presence of a living *Enallagma* individual at a station

Table 1. Comparisons of the percentages of perch height use by: (A) *Enallagma* spp., (B) *Perithemis tenera*, and (C) *Pachydiplax longipennis* when individuals perched alone, in the presence of living interspecifics, or in the presence of preserved and mounted decoys of *P. tenera* (behind the 12 cm perch) or *P. longipennis* (behind the 30 cm perch). Bracketed percentages denote the location of the decoy. We used χ^2 Goodness-of-fit tests to test for preferences for particular perch heights when alone, and to compare patterns of perch use in the presence of other live odonates (expected distributions of co-occurrence derived from independent probabilities of perch use – see methods). A significant result signifies a perch-height shift in response to the presence of the other species. We used χ^2 contingency tests to compare perch use in the presence of decoys with perch use in the absence of decoys. — ***: $p < 0.0001$; **: $p < 0.01$; *: $p < 0.05$, and n.s.: not significant; $df = 3$ for all χ^2 tests.

	Percentage of perch use at four perch heights				χ^2
	3 cm	12 cm	21 cm	30 cm	
A. <i>Enallagma</i> spp.					
Alone ($n = 349$)	51.0	41.6	6.0	1.4	260.50 ***
With live <i>P. tenera</i> ($n = 212$)	67.0	27.4	2.3	3.3	9.35 *
With live <i>P. longipennis</i> ($n = 15$)	20.0	66.7	13.3	0.0	6.57 n.s.
<i>P. tenera</i> decoy trials:					
Decoy absent ($n = 141$)	27.0	67.8	3.5	0.7	
Decoy present ($n = 102$)	53.9	[45.1]	0.0	1.0	20.59 **
<i>P. longipennis</i> decoy trials:					
Decoy absent ($n = 208$)	67.3	23.1	7.7	1.9	
Decoy present ($n = 127$)	47.2	18.1	19.7	[15.0]	35.02 ***
B. <i>Perithemis tenera</i>					
Alone ($n = 996$)	0.2	51.1	41.2	7.5	742.20 ***
With live <i>Enallagma</i> ($n = 212$)	0.0	40.6	51.9	7.5	6.17 n.s.
With live <i>P. longipennis</i> ($n = 15$)	0.0	70.3	27.0	2.7	11.57 **
<i>P. tenera</i> decoy trials:					
Decoy absent ($n = 404$)	0.3	48.5	44.3	6.9	
Decoy present ($n = 592$)	4.6	[77.9]	14.3	3.2	135.60 ***
<i>P. longipennis</i> decoy trials:					
Decoy absent ($n = 592$)	0.2	52.9	39.0	7.9	
Decoy present ($n = 584$)	5.1	51.7	38.7	[4.5]	33.69 ***
C. <i>Pachydiplax longipennis</i>					
Alone ($n = 182$)	0.0	0.0	14.3	85.7	367.7 ***
With live <i>Enallagma</i> ($n = 15$)	0.0	0.0	40.0	60.0	9.23 *
With live <i>P. tenera</i> ($n = 74$)	0.0	0.0	9.5	90.5	0.14 n.s.
<i>P. tenera</i> decoy trials:					
Decoy absent ($n = 103$)	0.0	0.0	22.3	77.7	
Decoy present ($n = 52$)	0.0	[1.9]	25.0	73.1	2.49 n.s.
<i>P. longipennis</i> decoy trials:					
Decoy absent ($n = 79$)	0.0	0.0	3.8	96.2	
Decoy present ($n = 87$)	0.0	1.1	18.4	[80.5]	9.78 *

had no effect on perch use by *P. tenera* males (Table 1B). However, the presence of a living *P. longipennis* male perched at a station caused male *P. tenera* to shift to lower perches, increasing their use of 12 cm perches to 70.3% of perch events (Table 1B).

The presence of a male *P. longipennis* decoy positioned behind the 30 cm perch had a similar effect. Male *P. tenera* shifted to lower perches in the presence of the *P. longipennis* decoy, using the 3 cm more frequently (5.1%) and the 30 cm perch less frequently (4.5%) than they did when decoys were absent (0.2% and 7.9% respectively; Table 1B). However, use of 12 cm and 21 cm perches were similar across these treatments (Table 1b). In addition, male *P. tenera* used stations with and without *P. longipennis* decoys at equal frequency ($n = 584$ and 592 , respectively; $\chi^2 = 0.01$, $df = 1$, n.s.).

Male *P. tenera* showed dramatic, aggressive responses to the presence of a conspecific decoy. They attacked the decoys, hovering above them and then quickly 'tagging' them with their legs. Eventually, they often perched directly on the decoy. In fact, perching on decoys ultimately accounted for 59% of all *P. tenera* perch events at stations with conspecific decoys. When these 'on decoy' events are scored as perches at 12 cm, there is a significant difference in the distribution of perch use between 'decoy present' and 'no decoy' treatments (Table 1B). Even if the total number of perch events observed at 12 cm (on wooden perches and on the decoys) is halved to correct for the two perches available at this height, there is still a significant increase in the use of 12 cm perches relative to 'decoy absent' stations ($\chi^2 = 59.93$, $df = 3$, $p < 0.0001$). In addition, *P. tenera* used stations with conspecific decoys more frequently than stations without decoys ($n = 404$ and 592 , respectively; $\chi^2 = 35.49$, $df = 1$, $p < 0.0001$); further demonstrating a positive response to the presence of a conspecific.

Perch selection by *Pachydiplax longipennis*

Males perching alone at a station preferred the taller perches (21 cm and 30 cm) and never used the 12 cm or 3 cm perches (Table 1C; 'decoy absent' stations, pooled across trials and stations). There was no difference from morning to afternoon in the distribution of perch events ($\chi^2 = 0.06$, $df = 3$, n.s.) nor in the level of activity (87 perches in morning, 95 in afternoon; $\chi^2 = 0.35$, $p =$ n.s.). When *Enallagma* was present, *P. longipennis* shifted lower, towards *Enallagma*, and used the 21 cm perch more than expected by the null co-occurrence model (Table 1c). The presence of a living *P. tenera* perching at a station had no effect on *P. longipennis* perch use (Table 1C). Likewise, the presence of a *P. tenera* decoy had no effect on perch use by *P. longipennis* (Table 1C). However, *P. longipennis* used stations with *P. tenera* decoys less often ($n = 52$) than stations without decoys ($n = 103$; $\chi^2 = 16.78$, $df = 1$, $p < 0.001$).

The presence of a conspecific decoy behind the 30 cm perch caused a significant shift in *P. longipennis* perch use, reducing the percentage of 30 cm perch use from 96.2% ('decoy absent') to 80.5% ('decoy present'; Table 1C). However, *P. longipennis* used stations with and without conspecific decoys with equal frequency ($n = 87$ and 79 , respectively; $\chi^2 = 0.39$, $df = 1$, n.s.).

DISCUSSION

The goal of this experiment was to determine whether interspecific and intraspecific interactions affect perch selection by three odonate taxa common to ponds in South Carolina: *Enallagma* spp., *Perithemis tenera*, and *Pachydiplax longipennis*. *Enallagma* preferred low perches (3 cm), *P. tenera* intermediate perches (12 cm and 21 cm) and *P. longipennis* tall perches (30 cm). There is strong evidence that asymmetrical, interspecific interference competition reinforces niche partitioning for perch height among these taxa.

For example, *Enallagma* showed a significant perch-height shift in the presence of *P. tenera*. *Enallagma* used 3 cm and 12 cm perches when alone, but shifted to primarily using the 3 cm perches when either live or decoy *P. tenera* were present. The response to decoys is particularly instructive. Because decoys were placed 10 cm behind a perch, all perches were still available for use. Thus, the shift in perch use by *Enallagma* can be attributed to interference competition from *P. tenera*, rather than pre-emptive resource use. In addition, *Enallagma* used stations less frequently when *P. tenera* decoys were present. So, *Enallagma* avoided stations with *P. tenera* decoys and shifted to lower perches in the presence of live and decoy *P. tenera*. Also, *Enallagma* used lower perches at higher frequency during morning trials, when *P. tenera* was most active. This is an asymmetrical interaction, because *P. tenera* neither avoided stations with *Enallagma* nor shifted perch sites in its presence.

These quantitative patterns are consistent with the few observed incidences of direct interspecific interactions between these taxa. Although *Enallagma* was never observed attacking *P. tenera*, there were several occasions when *P. tenera* attacked a perched *Enallagma* until it moved from a perch. *P. tenera* hovered above *Enallagma* and then looped down and 'tagged' it with the legs. It seems unlikely that these were instances of misidentification, where *P. tenera* males briefly pursue other insects that fly into their territory (sensu Shultz & Switzer 2001). *Enallagma* spp. are blue, slender, and hold their wings above their backs at rest. They look nothing like *P. tenera*, and these differences would be readily apparent while *Enallagma* is perching. Rather, the repeated attacks are more indicative of direct and purposeful interspecific aggression, consistent with the report of Bick & Bick (1963) who observed *P. tenera* driving *E. civile* from its territory.

P. tenera and *P. longipennis* also engaged in asymmetrical interference competition for perch sites. However, the asymmetry was also affected by the scale of the response. For instance, *P. longipennis* tended to avoid stations with a *P. tenera* decoy, perching at these stations half as often as at stations without a *P. tenera* decoy. This was a species-specific response, because *P. longipennis* showed no aversion to stations containing a conspecific decoy. However, once perched within a station, perch height selection by *P. longipennis* was unaffected by either live or decoy *P. tenera*. In contrast, *P. tenera* showed the opposite response across spatial scales. *P. tenera* used stations with and without *P. longipennis* decoys with equal frequency. At a small scale, however, perch height selection by *P. tenera* within a station was affected by the presence of *P. longipennis*. When alone, *P. tenera* used the 12 cm and 21 cm perches in roughly equal frequency, used the 30 cm perch occasionally,

and never used the low 3 cm perches. This aversion to 30 cm perches contrasts with the results of Switzer & Walters (2001), who found that 15 cm and 30 cm perches were used in equal frequency. In the presence of live or decoy *P. longipennis*, *P. tenera* either used the 12 cm perch more frequently than the 21 cm perch (live *P. longipennis* present) or used the low 3 cm perch and reduced use of the 30 cm perch (*P. longipennis* decoy present). Both patterns suggest a perch-height shift by *P. tenera* to lower perches when *P. longipennis* are present.

So, there were asymmetrical competitive interactions between taxa using neighboring perch-heights. Larger neighbors were unaffected by the presence of smaller neighbors, but smaller species shift to lower perches in the presence of larger species. As such, this experiment supports the hypothesis that interspecific competition structures communities in a size-dependent manner (Warren 1964; Williams 1976; Corbet 1999: 337). However, there is one interspecific interaction that does not conform to this pattern. When live or decoy *P. longipennis* were present, *Enallagma* shifted towards them to higher perches. Likewise, when *Enallagma* was present at a station, *P. longipennis* shifted towards them to lower perches. The response by *Enallagma* could indicate competitive release. If *P. tenera* avoids *P. longipennis*, then the presence of *P. longipennis* would reduce *P. tenera* perch activity at a station and might allow *Enallagma* to shift to higher perches – even perches higher than those used by it in isolation. The shift by *P. longipennis* is more difficult to explain. Since there is no evidence that perch height selection by *P. longipennis* was affected by competition from *P. tenera*, ‘competitive release’ can not be invoked. In any case, the sample size was very small for these interactions ($n = 15$) and any interpretation is probably premature. Additional experiments using *Enallagma* decoys are necessary to examine this effect more explicitly.

Intraspecific interactions are also species specific. Male *P. tenera* responded aggressively to the presence of conspecific decoys. They visited decoy stations more frequently than those without conspecific decoys, they attacked decoys, and they even perched directly on the decoys. In fact, *P. tenera* perched on the conspecific decoys 352 times in the 592 perch events at these stations (59.4%); well in excess of its use of 12 cm perches at stations without decoys (48.5%). In contrast, *P. tenera* only perched on *P. longipennis* decoys seven times in 593 perch events (1.2%), well below the rate at which it used 30 cm perches in isolation (7.9%). So, although *P. tenera* showed no aggression towards larger species and generally avoided them, it aggressively attacked conspecifics and smaller species (*Enallagma* spp. in this study). This confirms the results of Schultz & Switzer (2001), who found that *P. tenera* males rarely pursue larger odonates that invade their territory.

In contrast, *P. longipennis* showed a more subtle response to conspecifics. They used stations with and without conspecific decoys with equal frequency. However, the presence of a conspecific decoy behind the 30 cm perch caused them to shift to lower perches. They were more passive than *P. tenera*; they never perched on either *P. longipennis* or *P. tenera* decoys, and rarely attacked other species.

In conclusion, perch height selection by *Enallagma* spp., *P. tenera*, and *P. longipennis* is structured by asymmetric interference competition. Larger species use higher perches and competitively displace smaller species to lower perches. Intraspecific

interactions in *P. tenera* are strongly antagonistic; consistent with the strong territoriality these males exhibit as they defend oviposition sites. Intraspecific interactions in *P. longipennis* are less dramatic, resulting in a shift to lower perches when a conspecific decoy is present. Given the importance of perch site location to reproductive success (in *Perithemis*, in particular), these competitive interactions may represent important selective pressures and not just passive and transient behavioral responses.

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