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PERCH SELECTION BY MALE DRAGONFLIES (ODONATA, ANISOPTERA) RELATED TO COMPETITIVE ABILITY AND SPECIES COMPOSITION

by

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ABSTRACT

PERCH SELECTION IN MALE DRAGONFLIES (ODONATA, ANISOPTERA) RELATED TO COMPETITIVE ABILITY AND SPECIES COMPOSITION

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Old Dominion University, 2015
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Males of many species of dragonflies (Odonata, Anisoptera) establish territories in aquatic habitats where they compete with other males for access to food and females. Territorial males typically perch on emergent vegetation and chase rival males who intrude into their territories. This dissertation research examined the role of male size in perch height selection, position on the perch, and competitive ability. Four hypotheses were tested: 1) Dragonfly species would vary by size and that territorial species would show sexual size dimorphism (SSD), 2) Perch height selection would be related to dragonfly size, 3) Position on the perch would be related to male size, with larger males selecting perch tops and smaller inferior competitors choosing the sides of perches, and 4) Intraspecific competition would be more important than interspecific competition. Research was conducted at four lakes in southeastern Virginia from 2011-2014. For size measurements, male and female dragonflies were captured and measured for total body length, abdomen length, cerci length, forewing length and width, hindwing length and width and fresh mass. For perching experiments, alternating short (30cm above waterline) and tall (90cm above waterline) bamboo perches were placed in two rows, 0.5m and 2.0m from the shore. Any dragonflies that alighted on perches were recorded for species, gender, perch position and length of occupancy. Any interactions with conspecific or heterospecific dragonflies were recorded. Results showed that dragonfly males varied significantly among species in all parameters measured, and SSD was found for some parameters for some of the species. In particular, females of several species had greater forewing and hindwing widths than males, perhaps related to selection for energy conservation in females. There was no association between dragonfly size and perch height selection. Four species frequently perched on the sides rather than the tops of perches, and these species tended to be poor competitors who lost more contests than they won. The number of intraspecific and interspecific contests did not differ for any species. Neither dragonfly size nor residency on a perch influenced contest outcomes. Overall, these results revealed that dragonfly community interactions were dynamic and did not follow simple rules.

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CHAPTER 1

INTRODUCTION

The order Odonata, dragonflies and damselflies, is a group of hemimetabolous insects (those with aquatic nymphs and incomplete metamorphosis). They are considered one of the oldest groups of extant insects, going back to the Lower Permian era about 250 million years ago (Corbet, 1999; Grimaldi & Engel, 2005). A few hundred million years of evolution have allowed the group to diversify in habitat selection for nymphs and adults, mating habits, and behaviors, such as territoriality.

Both immature and adult stages are voracious predators. Adults eat other flying insects, especially mosquitoes, and are known to be cannibalistic. Predators of adult dragonflies include several bird families, amphibians, snakes, spiders, wasps, and other insects (Westfall & Tennessen, 1996; Corbet, 1999).

Odonates mate either in flight or while perching at varying distance from the water (Corbet, 1980; Westfall & Tennessen 1996). Before mating takes place, males must transfer sperm from the sperm duct located on the abdominal segment nine to the copulatory organ, located on the second abdominal segment. Then upon encountering a female, he clasps her by the back of the head with his caudal appendages, the cerci. At this point, they are said to be in tandem. The female then swings her abdomen up to meet the male’s genitalia so that the sperm may be transferred to her spermatheca (Corbet, 1980; Westfall & Tennessen, 1996). This position resembles a heart-shaped loop, characteristic of Odonata.

Since the immature stages of the vast majority of odonate species are aquatic, the eggs must be oviposited in or near water (Westfall & Tennessen, 1996; Corbet, 1999). There are several techniques for oviposition that are used depending on the species. Females may deposit eggs alone or in tandem. Males of many species in the family Libellulidae may guard the females during oviposition. Mate guarding is beneficial for many odonates because many species are capable of sperm competition among males (Corbet, 1999).

Males of many libellulid species are territorial and often defend perches within their territories. Overall, libellulids tend to show a large variation in the amount of time spent in any given territory (Koenig, 1990; Switzer 2002). Successful outcomes when defending territories have been attributed to fat content, and immunocompetence, age or body size (Suhonen et al., 2008). Important benefits of territoriality for male odonates include increased access to mates (Keonig, 1990; Serrano-Meneses et al., 2008a) and food (Baird & May 1997, 2003). Females benefit from ovipositing in high quality territories, which may increase offspring survival (Suhonen et al., 2008). Females also benefit from decreased harassment from other males while ovipositing within their mate's territory (Keonig, 1990).

Sexual Size Dimorphism

Dragonflies vary widely in size, both intra- and inter-specifically, and size affects many aspects of their lives, including perch selection and territoriality in males and fecundity in females. Sexual size dimorphism (SSD) refers to the condition of males and females exhibiting different sizes, and dragonflies and damselflies can show a large range in SSD. Some species exhibit a male-biased SSD, others may exhibit a female-biased SSD, while yet other species may be monomorphic for the same size character (Serrano-Meneses et al., 2008a).

In species where there exists a male-biased SSD, this size difference should increase with increasing body size. However, in species with larger females, the SSD should decrease with increasing body size. This allometric relationship is called Rensch's rule, and has been found to exist in a wide range of taxa (Abouheif & Fairbairn, 1997; Serrano-Meneses, 2008b). For dragonflies, there has been some support for Rench's rule (Johansson et al., 2005), but it has also not been supported with other studies (Serrano-Meneses et al., 2007, 2008b).

There are three hypotheses about the occurrence of sexual dimorphism in odonates. The most prominent hypothesis is that sexual selection causes an increase in the size of the sex that competes with one another the most. For odonates, especially those that are territorial, males are constantly competing with each other for females and in many cases, the largest males secure the highest quality territories and therefore more females (Serrano-Meneses, 2008a). This would lead to a male-biased SSD, because the largest males would be selected for by the females (Johansson et al., 2005). Larger males may also be favored in general due to the ability to coerce females into mating with them (Serrano-Meneses et al., 2008a). However female dragonflies may be able to overcome coercion (Rüppell & Hilfert-Rüppell, 2013). Conversely, small males may be selected for based on increased agility, which increases probability of winning aerial contests. This would lead to a female-biased SSD or an absence of SSD due to the relatively larger females and smaller males (Johannson et al., 2005, Serrano-Meneses et al., 2008a, 2008b).

Another hypothesis for the occurrence of SSD is that large females will be selected for due to the increased fecundity (Serrano-Meneses, 2008a). Though limited, there have been a few studies that show a positive relationship between female odonate size and fecundity (Koenig & Albano, 1987; Crowley, 2000, Crowley & Johansson, 2002). Specifically, large female *Plathemis lydia* have been shown to have increased lifetime reproductive success (Koenig & Albano, 1987).

Finally, SSD has also been attributed to differential niche utilization between males and females (Serrano-Meneses et al., 2008a). Specialization for different resources is expected to lead to size dimorphism. Though mostly theoretical for odonates, it is known that males and females may select different habitats (Corbet, 1999), but it is not known whether this leads to specialization on different food resources and the development of SSD (Serrano-Meneses et al., 2008a). Both males and females increase in mass from emergence to maturity, with females gaining mass in the abdomen and both genders gaining mass in the thorax (Anholt et al., 1991).

SSD in Libellulidae

In general, libellulids exhibit a male-biased SSD (Serrano-Meneses et al., 2008a), which is mainly attributed to the territorial nature of libellulid species (Annholt et al., 1991, Johansson et al., 2005). However, in species with aerial contests, SSD may not exist or may be female-biased due to the advantage of smaller, more agile males (Serrano-Meneses et al., 2008b).

Perch Height Selection Related to Size

Perch height selection may also be related to dragonfly size. Worthen and Jones (2006, 2007) found a positive correlation between mean body mass and perch height. Males may modify perching behavior depending on the other species in the area (Worthen & Patrick, 2004). For example, the medium-sized *Pachydiplax longipennis* dragonfly males significantly decrease their perch height when *Enallagama* damselflies are present, while the small dragonfly species *Perithemis tenera* has no effect on *P. longipennis* perch selection. Both intraspecific and interspecific interactions influence perch height and position selection. *P. longipennis* males avoid intraspecific decoys, and living and decoy *P. longipennis* cause both *Enallagma* and *P. tenera* to shift in perch height preferences (Worthen & Patrick, 2004).

Perch location selection

One study found that the small species *Perithemis tenera* prefers to perch farther from the shore than the oviposition sites in their territories, but show no preference in perch height (15cm versus 30cm high perches) (Switzer & Walters, 1999). This study also found that neighbors of territorial males influence perch position. Specifically, neighbors that are more than 5m away cause males to perch on the side of its territory that is closer to that neighbor, and neighbors less than 5m away cause males to perch at the far side away from these neighbors. Perching away from neighbors may increase efficiency for territory defense while also maximizing female encounter rate (Switzer & Walters, 1999).

Territorial Contests and Size

Fights over territories can incur many costs for odonates, including wing damage or loss of life in some cases (Rüppell & Hilfert-Rüppell, 2013). Fights may end when the male that can outlast the other, wins. This may result from winners having larger fat reserves than the opponent, which become depleted after several competitive bouts (Suhonen et al., 2008). Besides being energetically costly, competition over territories can increase the susceptibility to pathogens and parasites (Suhonen et al., 2008). Finally, territoriality can increase a male odonate's chances of being eaten by a predator (Suhonen et al., 2008).

Worthen and Jones (2006, 2007) found that male odonate size was the most important factor in determining competitive outcomes. In their study, larger species were more successful than smaller species in displacing perching heterospecifics. Dragonfly communities vary in species composition and size range from site to site (personal observation) and community dynamics are therefore likely to vary among locations. For the study represented in this dissertation, it was expected that odonate males would exhibit differences in competition ability related to the other odonate species that are present.

Intraspecific contests

Many studies on male territory contests in dragonflies have focused on intraspecific competition. Lutz and Pittman (1970) found that intraspecific contests are more frequent than interspecific interactions in their study of a community with 18 odonates. Within species, individuals may show a large variation in their abilities to secure and defend territories (Tsubaki & Ono, 1987; Koenig, 1990; Switzer, 2002a; Switzer, 2002b). Factors that determine the winner of contests include body size, age, residency status, and energy reserves (Switzer, 2004; Suhonen et al., 2008). The importance of these factors is not consistent across species or even within a species (Switzer, 2004).

Body size influences contest outcomes in some species, but not in other species (Switzer, 2004; Suhonen et al., 2008). Tsubaki and Ono (1987) found that large male *Nannophya pygmaea* are able to occupy higher quality territories than smaller males. This study also found that large males have higher mating success in a lifetime. However, this was probably not due to a size difference but because the larger males had longer lifespans and thus were competing on days that were more conducive to activity (i.e. sunny days) which led to more matings per individual (Tsubaki & Ono, 1987). McCauley (2010) found that larger *Pachydiplax longipennis* are competitively dominant and chase away smaller conspecific males, which are most likely to disperse. A study with another species, *Orthetrum japonicum*, showed that contest winners have larger body widths, but the main factor in a successful outcome was being a resident instead of an intruder to the territory (Kasuya et al., 1997). Also, Miller (1983) found that larger males are more successful in holding territories than smaller individuals (Tsubaki & Ono, 1987). In contrast, other studies on *Perithemis tenera* (Switzer, 2002a; 2002b; 2004) and *Macrothemis imitans* (Mourao & Peixoto, 2014) have shown no body size differences between contest winners and losers (Switzer, 2002b; Switzer, 2004; Mourao & Peixoto, 2014). Also, in *Sympetrum rubicundulum*, male size has no influence on survival, mating success, or the ability to defend territories (Van Buskirk, 1986; 1987).

Several studies have shown age to be a factor in the outcome of territorial disputes (Suhonen et al., 2008). Tsubaki and Ono (1987) found that young *N. pygmaea* often overtake older males in contests. As a result, the older males are forced to occupy territories of lower quality (Tsubaki & Ono, 1987). Age is also related to competitive ability in *Perithemis tenera* (Switzer, 2002b; Switzer, 2004). Specifically, older males lose to younger individuals, presumably because these older individuals have had to fight more for their higher quality territories (Switzer, 2002b) and energy reserves are important in determining the contest outcome (Koenig, 1990; Switzer, 2004).

The factor that has received much of the attention on territory contests is residency (Switzer, 2004). In one study, resident males of *Macrothemis imitans* won 100% of territory contests, even though they were not different from non-resident males in any measured physical trait (Mourao & Peixoto, 2014). Also, residency is more important than body size in *Orthetrum japonicum* (Kasuya et al., 1997) and *Sympetrum rubicundulum* (Van Buskirk, 1986; 1987) for determining the outcome of territorial disputes (Kasuya et al., 1997).

Interspecific contests

Aggressive interspecific interactions frequently occur among species that are morphologically similar. *Pachydiplax longipennis* chases three larger species, *Libellula incesta*, *L. cyamae*, and *Erythemis simplicollis*, perhaps because they have similar pruinescent coloration (Robey, 1975). *Libellula pulchella* is most aggressive to heterospecifics of its own size (Pezalla, 1979). The small wasp mimic *Perethemis tenera* chases other insects similar in size and color, including horse flies and butterflies, but not other odonates that do not resemble it (Schultz & Switzer, 2001).

Several studies by Worthen et al. focusing on a guild of libellulids, found that perch height selection is heavily affected by interspecific competition. These studies show that larger species perch on taller perches and smaller species use shorter perches, which was attributed to differing wind speeds at different heights (Worthen & Jones, 2006; 2007), but also competitive interactions significantly affect perching heights (Worthen & Patrick, 2004; Worthen & Jones, 2007).

Worthen and Patrick (2004) studied two libellulids, *P. tenera* and *P. longipennis* for perch selection, along with two *Enallagma* species. When perching alone, the perch height is correlated with body mass as *Enallagma* species choose the lowest perches, *P. tenera* choose intermediate perches, and *P. longipennis* perches on the tallest perches. Interspecific interference also affects perch heights of each species. Specifically, *P. tenera* causes the smaller taxa, *Enallagma*, to shift to lower perches and *P. longipennis* also causes *P. tenera* to shift to lower perches (Worthen & Patrick, 2004).

Worthen and Jones (2007) studied a community of eleven libellulid species and also found that niche partitioning occurs due to competitive abilities based on body size. Specifically, larger species always displace smaller species, and smaller species avoid larger species (Worthen & Jones, 2007).

Hypotheses

The following hypotheses were addressed for this dissertation:

Hypothesis 1:

Species will vary by size and there will be SSD in territorial species.

Hypothesis 2:

Perch height is related to dragonfly size. Specifically, larger dragonflies will prefer to perch near the top of the perches and on taller perches.

Hypothesis 3:

Position on the perch (top versus side) is related to competition among the species. Larger dragonflies with superior competitive abilities will be more successful in securing positions at the top of the perch, and smaller inferior competitors will perch on the side.

Hypothesis 4:

Interspecific competition is less intense than intraspecific competition.

CHAPTER 2

METHODS

Dragonfly size parameters

During 2013-2014 seasons, dragonflies were captured, marked and released in order to measure and record several size parameters. Specimens were caught with standard aerial insect nets, identified to species and gender, and measured with digital calipers to the nearest 0.01cm. Parameters measured included lengths of total size, abdomen, cerci length, forewing and hindwing lengths and widths, and wet mass. Specimens were then put inside an insect envelope and placed on a digital scale in order to measure weight to the nearest 0.01g. Finally, each individual was photographed and released in the same general area as it was captured.

Each specimen was marked with a unique number in a permanent marker color for each site, and each species had its own number series for each location. Different color markers were used for different sites to determine if any specimens moved from any site to another; however, this was never observed for any specimen or site.

Data Analysis

For 2013, the following parameters were measured for specimens collected: total length, abdomen length without cerci, abdomen length including cerci, forewing length, forewing width, hindwing length, hindwing width, and fresh mass. Data analyses were left out for this year because measurement tools were inconsistent and all measurement parameters were not taken for every individual throughout the season.

Table 1. Number of specimens marked and measured for all sites in 2013. (SH= Sleepy Hole; HC= Hoffler Creek, LW = Lake Whitehurst; SL= Stumpy Lake).

		SH	HC	LW	SL
B. gravida	M	0	3	0	0
	F	0	0	0	0
C. eponina	M	0	1	0	0
	F	0	2	0	0
E. simplicicollis	M	11	2	1	10
	F	1	0	3	20
L. incesta	M	5	0	1	5
	F	0	0	1	0
L. needhami	M	0	4	0	0
	F	0	4	0	0
L. vibrans	M	0	1	0	12
	F	0	0	0	8
P. longipennis	M	27	0	13	0
	F	3	1	1	0
P. lydia	M	0	0	0	0
	F	0	0	0	0
P. tenera	M	2	0	1	0
	F	0	0	0	0

For 2014, the following parameters were collected from all specimens and used in analyses: total length, abdomen length, cerci length, abdomen with cerci length, forewing length, forewing width, hindwing length, hindwing width, and wet mass. Only three sites were visited during this season. The vast majority of specimens were from Stumpy Lake and Hoffler Creek with 69 specimens caught at each location, while Sleepy Hole only had six specimens caught there (Table 2). *Pachydiplax longipennis* and *E. simplicicollis* were caught at all three sites and *L. vibrans* was captured at both Hoffler Creek and Stumpy Lake. *Perithemis tenera, Libellula incesta* and *Plathemis lydia* were caught only at Stumpy Lake, while *Brachymesia gravida, Celithemis eponina,* and *L. needhami* were all caught only at Hoffler Creek (Table 2).

Table 2. Number of specimens marked and measured for all sites in 2014. (SH= Sleepy Hole; HC= Hoffler Creek, LW = Lake Whitehurst; SL= Stumpy Lake).

		SH	HC	SL
B. gravida	M	0	7	0
	F	0	2	0
C. eponina	M	0	5	0
	F	0	3	0
E. simplicicollis	M	1	10	2
	F	1	5	2
L. incesta	M	0	0	3
	F	0	0	1
L. needhami	M	0	16	0
	F	0	0	0
L. vibrans	M	0	1	12
	F	0	0	15
P. longipennis	M	2	12	2
	F	2	10	8
P. lydia	M	0	0	0
	F	0	0	2
P. tenera	M	0	0	8
	F	0	0	13

Perching experiments

For experiments during 2011-2013, perches were arranged in two rows of four perches, alternating tall (90cm high) and short (30cm high) perches. The first row (near shore) was 50cm from the water's edge and perches were arranged 50cm apart in the following order: tall, short, tall, short. The second row (open water) was 2m from the water's edge (1.5m from the first row) with the perches 50cm apart in the order: short, tall, short, tall. Therefore there were equal numbers of perches near and far shore, with alternating tall and short perches. Perches consisted of bamboo stakes that were very similar to natural perches in the habitat.

For each test session, perches were placed in the water in the morning around 10am and observed for two hours. Every dragonfly that landed on a perch was recorded for species, gender and any identifying characteristics (such as age or wing tear). Perch choice (including near or far shore, tall or short perch, top or middle of the perch) was recorded for each landing, and the length of time the dragonfly remained on the perch was noted. Behavior on the perch, such as obelisking (raising the abdomen in a defensive or thermoregulation posture) or "hopping" (flying off the perch very briefly and returning immediately) was described. Any interactions with other dragonflies that attempted to harass or displace the percher were recorded, and the outcome of any contests for the perch was noted.

Study sites included four lakes across the Hampton Roads area from Suffolk east to Virginia Beach. Perch observations at study sites were rotated so that each study site was visited early, mid and late season to detect any seasonal effects in species composition, species abundance or competitive ability. Perch experiments were carried out the same number of times for each site, while marking re-capture studies were done at random sites throughout the seasons (Table 3).

Table 3. Number of days each site was visited for perch experiments (P) and marking (M) during each year.

	SH	HC	LW	SL
2011	0	10P	0	0
2012	5P	5P	5P	5P
2013	3P, 6M	3P, 4M	3P, 4M	3P, 5M
2014	2M	6M	0	5M

Study locations

Experiments were conducted at the following locations (Figure 1) in the Tidewater area of Virginia:

Sleepy Hole Lake

Sleepy Hole Lake is a 5 acre lake located in Suffolk, Virginia (Figure 1). The lake was surrounded by a golf course and a patch of trees. Fish were common in the lake. Sleepy Hole Lake was visited five days in 2012, nine days in 2013, and two days in 2014. A total of 15 species were identified from this site (Table 4).

Lake Ballard

Lake Ballard is a 640 acre brackish lake created from a borrow pit and located in Portsmouth, Virginia, in the Hoffler Creek Nature Preserve (Figure 1). Fish have occasionally been collected in the lake although there is disagreement about whether it supports a fish population. Lake Ballard was visited ten days in 2011, five days in 2012, seven days in 2013, and six days in 2014. A total of 16 species were identified at this site (Table 4).

Lake Whitehurst

Lake Whitehurst is a 480 acre lake that is used as a water supply for Norfolk, Virginia (Figure 1). It is located in Norfolk near the Botanical Garden. The lake supported a healthy fish population. Lake Whitehurst was visited five days in 2012 and seven days in 2013. Nine dragonfly species were observed at Lake Whitehurst (Table 4).

Stumpy Lake

Stumpy Lake is a 278 acre lake located in Virginia Beach near the border of Chesapeake, Virginia (Figure 1). It was next to a golf course and ringed with trees. Fish were abundant in the lake. Stumpy Lake was visited five days in 2012, eight days in 2013 and five days in 2014. The dragonflies recorded from Stumpy Lake totaled 12 species (Table 4).

Figure 1. Locations of each study site. Sleepy Hole Lake in Suffolk, Hoffler Creek's Lake Ballard in Portsmouth, Norfolk Botanical Garden's Lake Whitehurst in Norfolk, and Stumpy Lake in Virginia Beach, VA.

Table 4. Number of species found at each site for years 2011-2013.

Species	SH	HC	LW	SL
Anax junius	x	x	x	x
Anax longipes		x		
Brachymesia gravida	x	x		
Celithemis eponina	x	x	x	x
Epiaeschna heros	x			
Epitheca princeps	x	x	x	x
Erythemis simplicicollis	x	x	x	x
Libellula incesta	x	x	x	x
Libellula luctuosa	x	x		
Libellula needhami	x	x		x
Libellula semifasciata		x		
Libellula vibrans	x	x		x
Pachydiplax longipennis	x	x	x	x
Plathemis lydia	x	x		x
Perithemis tenera	x	x	x	x
Tramea carolina	x	x	x	x
Tramea lacerata	x	x	x	x
TOTAL	15	16	9	12

Species descriptions

The following species were caught during mark-release-recapture studies in 2013-2014. The species are listed according to total length sizes from smallest to largest.

Amberwing, *Perithemis tenera* Say 1839, (average male total length 2.22 cm) is a tiny dragonfly that is often found around marshes, ponds and lakes. It is considered a wasp mimic and is often found perching away from water. This species, although common in my field sites, never participated in competitions over perches during experiments.

Blue dasher, *Pachydiplax longipennis* Burmeister 1839, (average male total length 3.77 cm) was the most common species at all field sites and regularly competed fiercely over perches. This species is frequently found in a wide variety of aquatic habitats and tends to perch near the shoreline.

Halloween pennant, *Celithemis eponina* Drury 1773, (average male total length 3.83 cm) is a very conspicuous dragonfly with bright red and black marked wings. It is common around marshes, lakes, and ponds and often perches on vegetation near the shoreline. Though not considered territorial (Corbet 1999), this species competed frequently on perches during experiments and was found at all field sites.

Common whitetail, *Plathemis lydia* Drury 1773, (male total length 3.8-4.8 cm; Beaton 2007) has a bright white body with dark bands across its wings. This species is common near aquatic habitats of varying sizes, but it was not very common at my field sites and never competed over experimental perches. It was found commonly only at Sleepy Hole in 2012 and Stumpy Lake in 2012 and 2014.

Eastern pondhawk, *Erythemis simplicicollis* Say 1839, is a medium sized species (average male total length 4.42 cm) that is common around ponds and lakes. It was observed at all field sites but alighted on perches during experiments infrequently. Female pondhawks were often found eating other dragonflies.

Four-spotted pennant, *Brachymesia gravida* (Calvert 1890), (average male total length 5.10 cm) is common near coastal areas in the eastern US and frequents lakes and ponds, even brackish water. Like *C. eponina*, this species was common at two field sites, Sleepy Hole and Hoffler Creek where it often competed over perches in experiments.

Needham's skimmer, *Libellula needhami* Westfall 1943, (average male total length 5.32 cm) is a bright red dragonfly that is found near coastlines in southeastern US. This species was very common at Hoffler Creek, but found at Sleepy Hole only in 2012 and at Stumpy Lake only in 2013. It regularly competed over perches at Hoffler Creek and Sleepy Hole.

Slaty skimmer, *Libellula incesta* Hagen 1861, (average male total length 5.32 cm) is a common species in pond and lake habitats. It occurred at all sites, except at Hoffler Creek it was only found during 2012.

Great blue skimmer, *Libellula vibrans* Fabricius 1793, is the largest species in the Libellulidae family (average male total length 5.99 cm). It is found around ponds and slow streams and swamps. This species was common only at one field site, Stumpy Lake, though it rarely alighted on experimental perches and perched most often on vegetation near the swampy side of this site.

CHAPTER 3

RESULTS

Size measurement data

In 2013, a total of 153 dragonflies was captured and released over 12 days. In 2014, a total of 146 dragonflies was captured and released over 16 days. One female *E. simplicicollis* was recaptured in 2013. There were seven recaptures in 2014, which were two male and two female *E. simplicicollis*, one male and one female *P. longipennis*, and one male *L. needhami*. All species were recaptured on the same date at the same site as the original capture. The recapture rate for each year was 0.01 and 0.05 for 2013 and 2014, respectively.

Table 5. F and P-values for 1-way ANOVA tests for males of all species caught in 2014 for each variable.

Variable	df	F	*p*
total length	7	13.695	<0.0001
abdomen length	7	258.513	<0.0001
cerci length	7	43.695	<0.0001
weight	7	147.205	<0.0001
forewing length	7	456.985	<0.0001
forewing width	7	122.48	<0.0001
hindwing length	7	488.416	<0.0001
hindwing width	7	121.107	<0.0001
abdomen with cerci	7	271.393	<0.0001

Results from a 1-way ANOVA indicated a significant difference among males caught in 2014 in all species for all measurements taken (Figures 2-9, Table 5). Gender differences for each parameter were tested with 1-way ANOVAs for each species. Gender measurements were significantly different for some species for total length (Figure 2), abdomen length (Figure 3), cerci length (Figure 4), fresh mass (Figure 5), forewing width (Figure 8) and hindwing width (Figure 9). No species showed gender differences in forewing length (Figure 6) or hindwing length (Figure 7). Gender differences were not tested for *P. lydia, L. needhami,* or *L. incesta* due to lack of enough males or females measured.

For the total length measurement, *P. tenera* was the smallest species and *L. vibrans* was the largest (Figure 2). Averages for males and females of *P. tenera* were 2.22 and 2.13 cm, respectively, which were significantly different (F=7.449, P= 0.013). *Pachydiplax longipennis* and *C. eponina* were the next largest species with male averages of 3.76cm and 3.83cm, respectively. Males of these species did not differ significantly (Tukey test P > 0.05). Males and females did differ in total length for *P. longipennis* (F= 16.074, P= 0.0003), but not for *C. eponia* (F= 0.229, P> 0.05). *Erythemis simplicicollis* was in the medium range for total size with an average of 4.42 cm for both males and females. Sizes of males of *B. gravida*, *L. needhami*, and *L. incesta* were not significantly different from each other with averages of 5.10, 5.32, and 5.32 cm, respectively. Total length for *L. vibrans* for males and females were 5.99 and 5.83 cm, respectively, which differed significantly (F= 5.09, P=0.033).

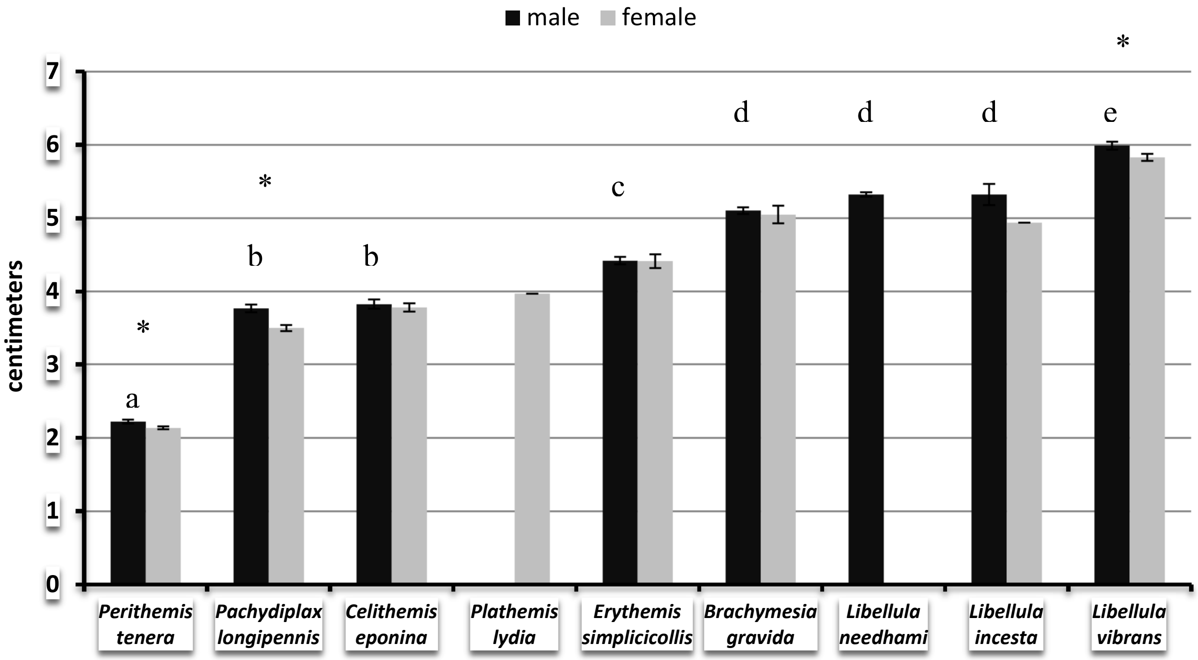

Figure 2. Average total length measurements (cm +/- SE) for all species in 2014. Different letters represent significant differences among males of each species. Asterisks represent significant differences between males and females of the same species.

Results for the abdomen length (not including cerci length) followed those for the total length (Figure 3). *Perithemis tenera* was the smallest at 1.21 cm for both males and females. There was no difference for males between *P. longipennis* and *C. eponina*, (Tukey test P>0.05) with averages of 2.36 and 2.46 cm, respectively. Females of *P. longipennis* and *C. eponina* were 2.15 and 2.41 cm on average, respectively. *Erythemis simplicicollis* was a medium-sized species averaging 2.85 cm for both males and females. There was no difference in male abdomen lengths of the large species *B. gravida, L. needhami,* and *L. incesta*. The males of these species had average abdomen lengths of 3.30, 3.33, and 3.38 cm, respectively. The largest species present was *L. vibrans*, with male and female abdomen lengths averaging 3.76 and 3.79 cm, respectively. The only species for which there was a gender difference was *P. longipennis* (F= 13.541, P= 0.001).

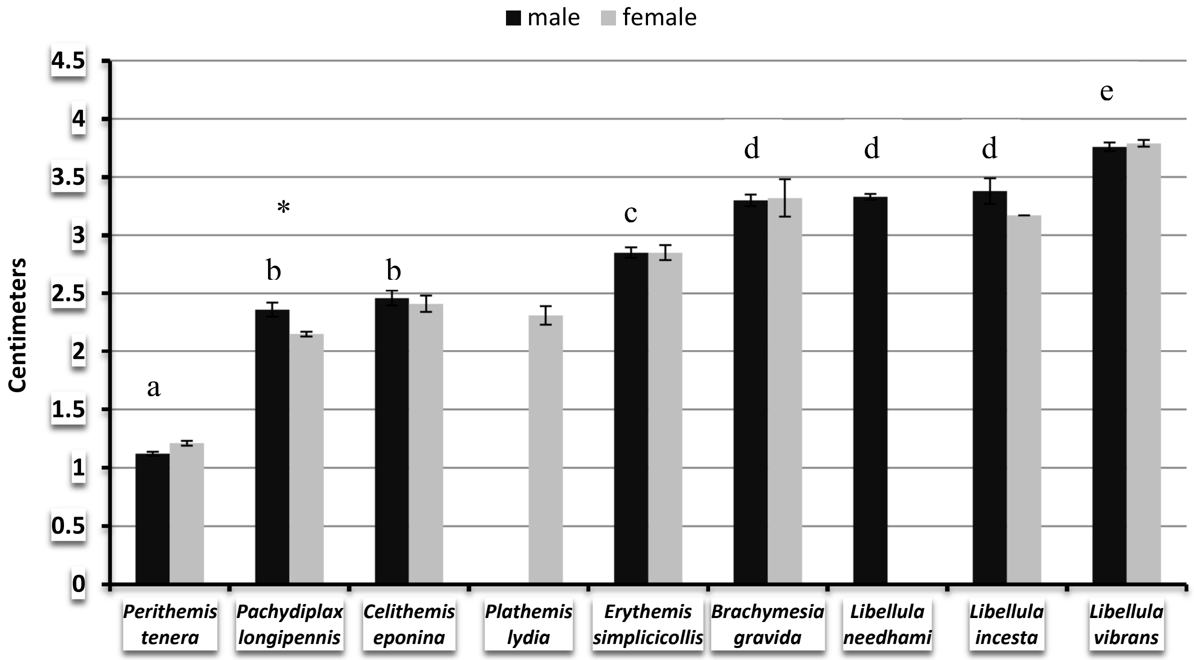

Figure 3. Abdomen length measurements (cm) for all species in 2014. Different letters represent significant differences among males of each species. Asterisks represent significant differences between males and females of the same species.

Measurements of cerci length showed the greatest number of gender differences among species (five out of seven species showed gender differences; Figure 4). For each of these species, the males had significantly longer cerci than females (*P. tenera*: F= 31.27, P<0.001; *P. longipennis* F= 72.351, P<0.000001; *C. eponia* F=32.24, P<0.001; *E. simplicicollis* F= 9.538, P=0.006; and *L. vibrans* F=58.134, P<0.001). *Brachymesia gravida* was the only species in which the females appeared to have longer cerci than the males and this difference seems large; however, statistical analysis failed to show a significant difference (F= 5.105, P=0.058).

For males, *P. tenera* had the smallest cerci, which were significantly different from all other species (Tukey test P<0.05). For the other species, there was overlap in the similarities of cerci lengths. From smaller to larger, *C. eponina, E. simplicicollis,* and *P. longipennis* male cerci did not differ from each other (Tukey test P>0.05), but the male cerci of *E. simplicicollis* and *P. longipennis* were significantly similar to *L. needhami* as well (Tukey test P>0.05). Finally, *L. needhami, B. gravida, L. incesta,* and *L. vibrans* did not show significant differences in cerci lengths (Tukey test P>0.05).

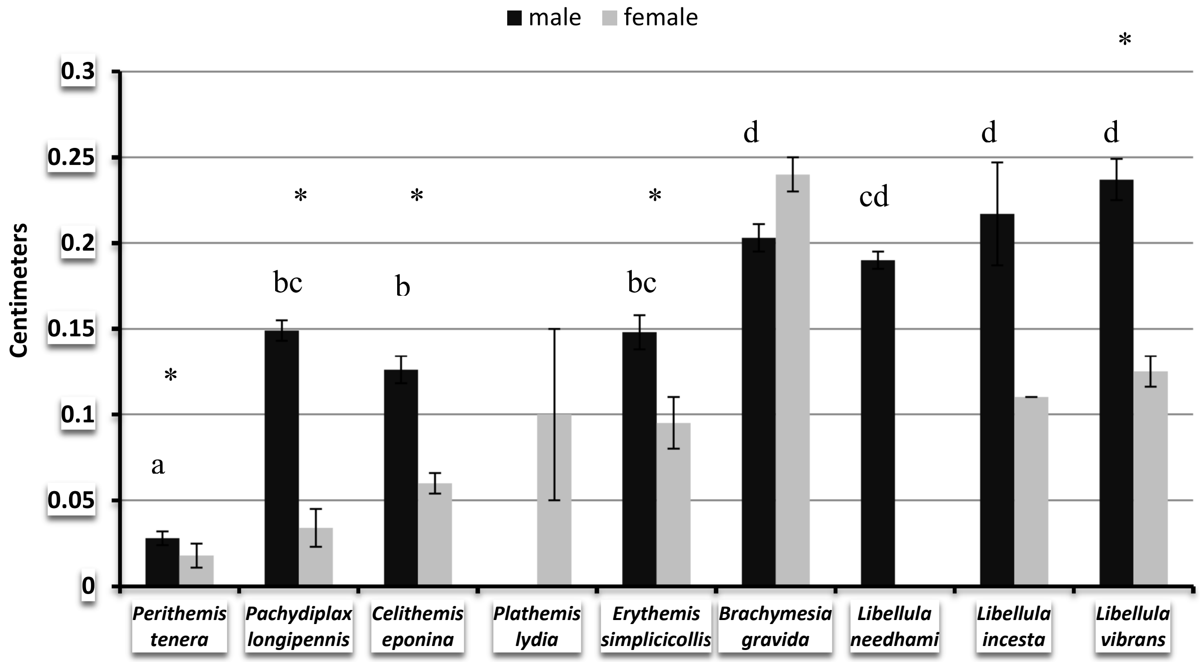

Figure 4. Cerci length measurements (cm) for all species in 2014. Different letters represent significant differences among males of each species. Asterisks represent significant differences between males and females of the same species.

Fresh mass measurement results show significant gender differences in two species (*E. simplicicollis*: F= 8.74, P= 0.008; *L. vibrans*: F= 11.63, P= 0.002) and females were heavier than males (Figure 5). Overall, *P. tenera* showed the lowest weight and *L. vibrans* weighed the most. *Pachydiplax longipennis, C. eponina* and *E. simplicicollis* did not differ from each other (Tukey test P>0.05). *Brachymesia gravida* was the next heaviest species and differed from all other species in fresh mass. Finally, *L. needhami* and *L. incesta* were not different in fresh mass from each other, but both weighed less than *L. vibrans*.

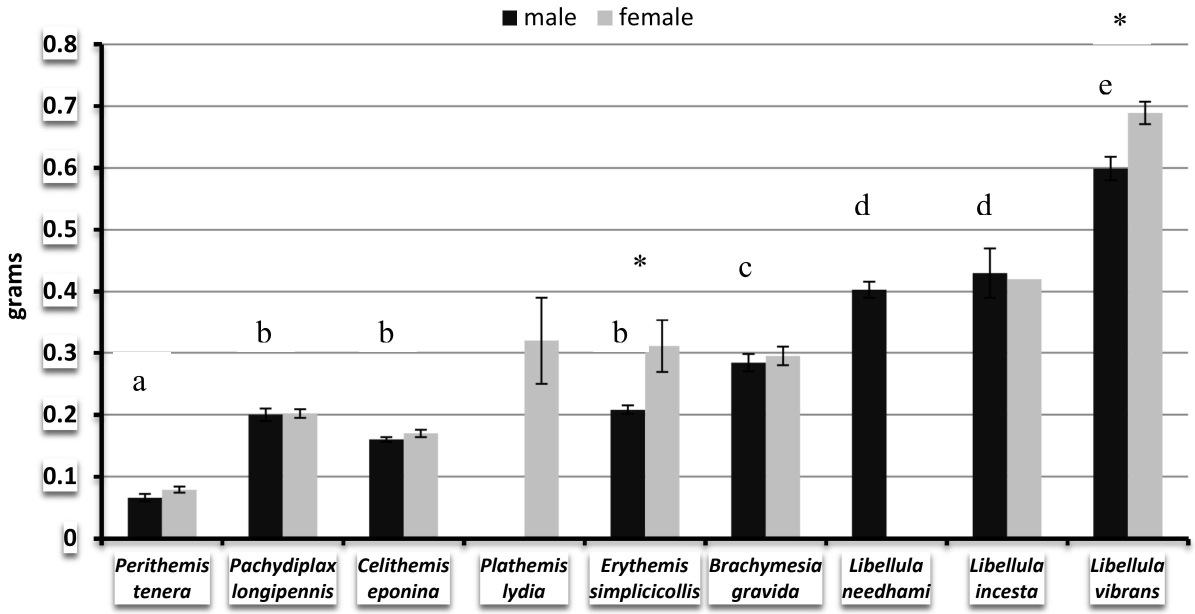

Figure 5. Fresh mass measurements (g) for all species in 2014. Different letters represent significant differences among males of each species. Asterisks represent significant differences between males and females of the same species.

Forewing and hindwing length measurements varied significantly among species for males, but showed no differences between genders (Figure 6-7) and displayed the same patterns across species. For males, *P. tenera* had the shortest wings followed by *P. longipennis*, which were significantly different from each other and all other species (Tukey test P<0.05). *Erythemis simplicicollis* and *C. eponina* males did not differ significantly from each other, nor did *B. gravida* and *L. needhami* (Tukey test P>0.05), but both groups differed from each other (Tukey test P<0.05). *Libellula incesta* males had the next longest wings, while *L. vibrans* had the longest wings of all species. These two species differed significantly from each other and from all other species (Tukey test P>0.05).

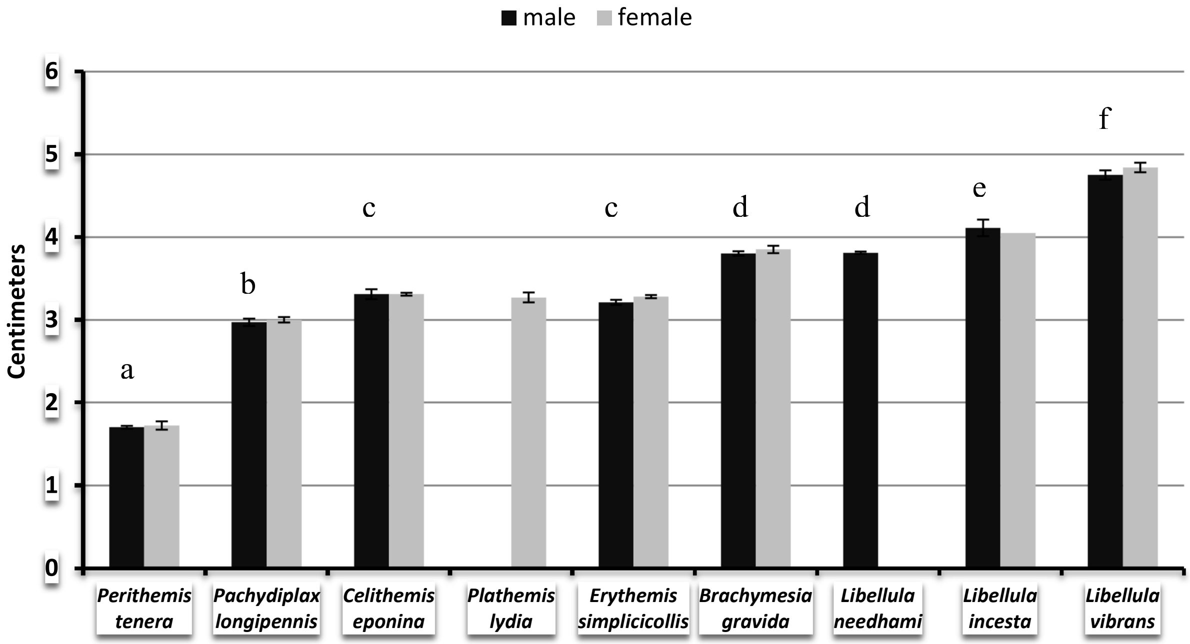

Figure 6. Forewing length measurements (cm) for all species in 2014. Different letters represent significant differences among males of each species. Asterisks represent significant differences between males and females of the same species.

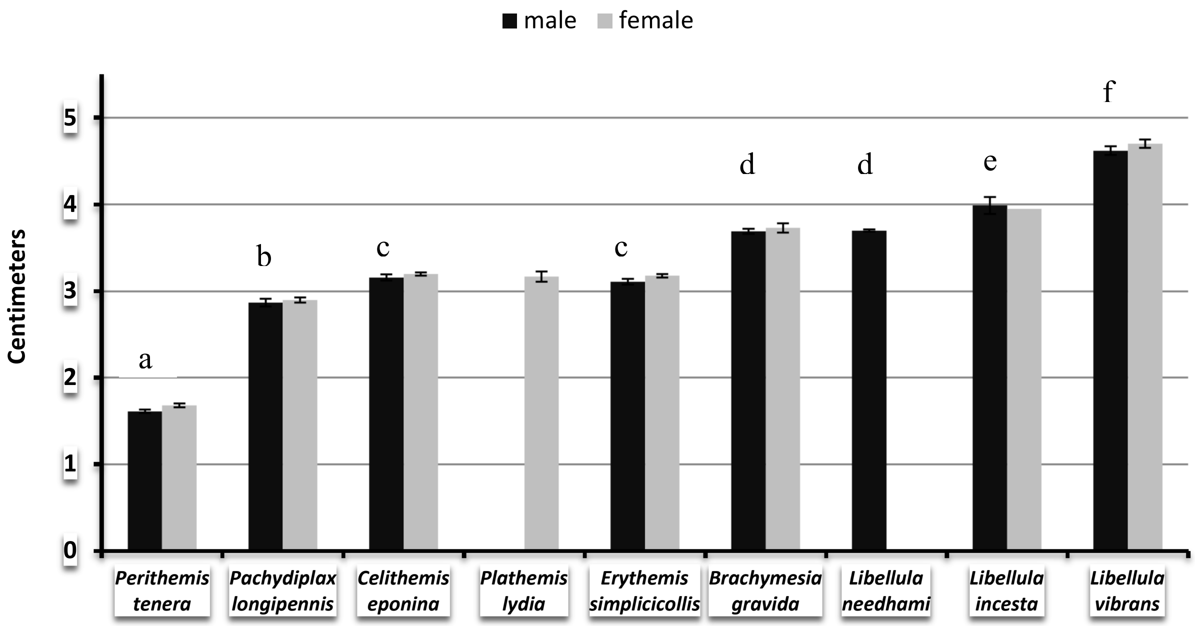

Figure 7. Hindwing length measurements (cm) for all species in 2014. Different letters represent significant differences among males of each species. Asterisks represent significant differences between males and females of the same species.

Width measurements for male fore and hindwings varied significantly among species. Males showed the same patterns among species for both forewing and hindwing widths. *Perithemis tenera* had the most narrow wings, *L. vibrans* had the broadest wings, and both species were different from all other species. Also, *P. longipennis* and *E. simplicicollis* were not different from each other for wing widths (Tukey test P>0.05). *Celithemis eponina, B. gravida , L. needhami, and L. incesta* did not show differences in wing widths, but were different from all other species (Figure 8-9).

There were significant differences between genders for fore and hindwing widths for some species, and both fore and hindwings showed the same patterns across species. *Perithemis tenera*, *P. longipennis*, and *B. gravida* all showed gender differences for both width measurements, while *E. simplicicollis* had gender differences only in forewing width (F= 6.247, P=0.022). In these species, females had significantly wider wings than males (Figure 8-9).

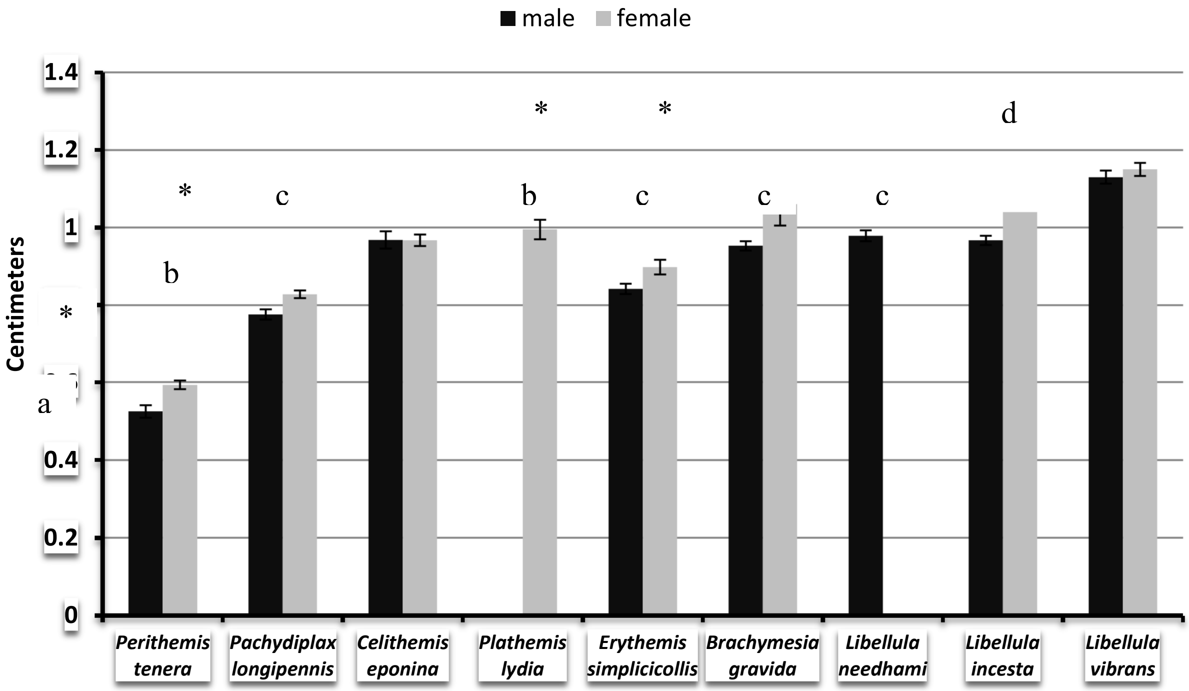

Figure 8. Forewing width measurements (cm) for all species in 2014. Different letters represent significant differences among males of each species. Asterisks represent significant differences between males and females of the same species.

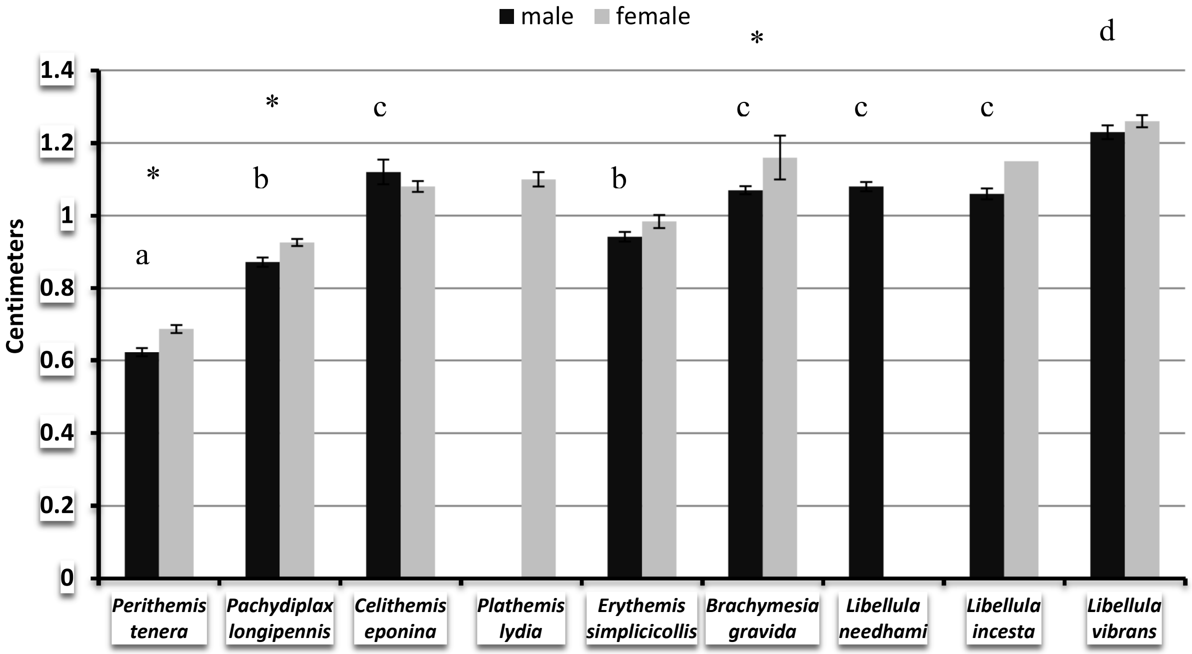

Figure 9. Hindwing width measurements (cm) for all species in 2014. Different letters represent significant differences among males of each species. Asterisks represent significant differences between males and females of the same species.

Perching results

There were no differences in perching events between the front and back line of perches for 2012 for any of the sites (paired t-tests: Sleepy Hole tall perches P= 0.065, short perches P= 0.34; Hoffler Creek tall perches P= 0.12, short perches P= 0.40; Lake Whitehurst tall perches P= 0.28, short perches P= 0.10; Stumpy Lake tall perches P= 0.34, short perches P= 0.11). There were also no differences between front and back lines at any of the sites for 2013 (paired t-tests: Sleepy Hole tall perches P= 0.55, short perches P= 0.23; Hoffler Creek tall perches P= 0.08, short perches P= 0.09; Lake Whitehurst tall perches P= 0.31, short perches P= 0.28; Stumpy Lake tall perches P= 0.21, short perches P= 0.17). However, there was a difference between front and back lines of perches for Hoffler Creek in 2011 (tall perches P= 0.024, short perches P=0.060), probably due to frequent shading of the front line of perches at this location.

There was a difference in species perching at the tops of perches for the different field sites. At Sleepy Hole and Hoffler Creek, there were six species vying over perches: *Pachydiplax longipennis*, *Brachymesia gravida, Celithemis eponina , Libellula needhami, Libellula incesta,* and *Erythemis simplicicollis* (Figures 10-14). In contrast, only *P. longipennis* and *L. incesta* were the main perching species at both Lake Whitehurst and Stumpy Lake (Figures 15-18). Of all perching species, *P. longipennis* and *C. eponina* were considered small species, *E. simplicicollis* was a medium-sized species, and *L. needhami* and *L. incesta* were large species (Figure 2). Although the tiny species *Perethemis tenera* was smaller than all the other species, it never perched on top of either short or tall artificial perches.

The small species *P. longipennis* seemed to be the most generalized perching species. It perched both on short and tall perches at all four sites. *Brachymesia gravida*, a large species, also perched on both short and tall perches at Hoffler Creek. At Sleepy Hole, *B. gravida* chose short perches in 2012 and tall perches in 2013.

The small species *C. eponina* perched most often on tall perches at both Sleepy Hole and Hoffler Creek for all years studied. The large species, *L. needhami,* also perched most often on tall perches at both Sleepy Hole and Hoffler Creek for all years studied.

The large species *L. incesta* perched most often on tall perches for most sites and years. At Sleepy Hole, Stumpy Lake, and Hoffler Creek, it perched most often on tall perches. At Lake Whitehurst, it perched on tall perches in 2012 and short in 2013. The medium-sized species, *E. simplicicollis* perched only on short perches at both sites.

These results do not support the first hypothesis, which predicted that small species would perch most often on short perches (30 cm) and large species would perch primarily on tall perches (90 cm).

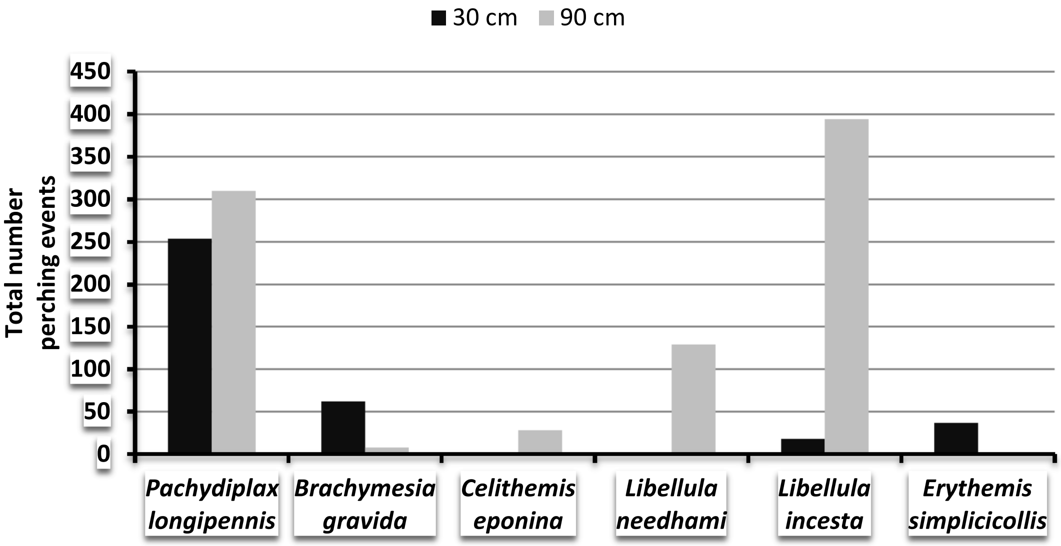

Figure 10. Total number of perching events at the top of perches at Sleepy Hole in 2012 for each species on short (30cm) and tall (90cm) perches.

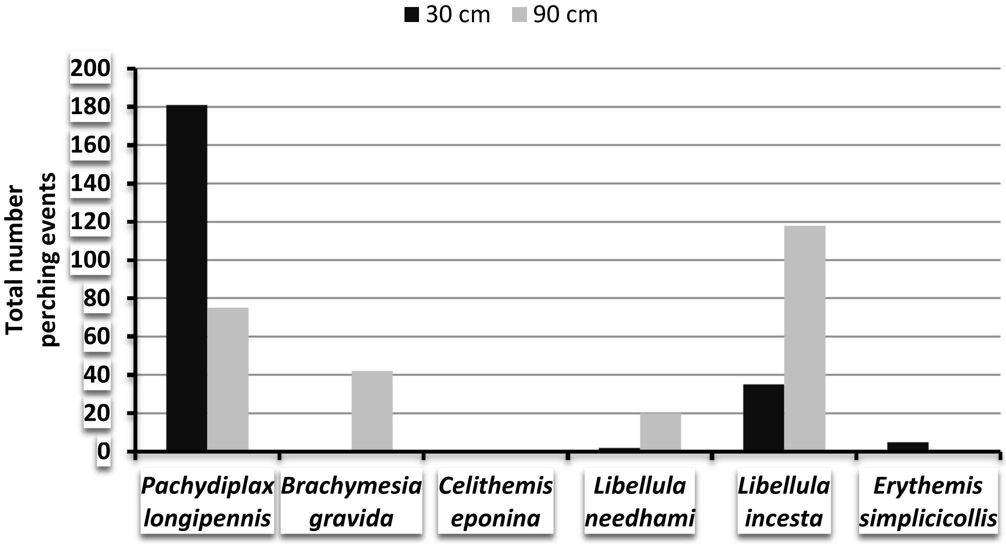

Figure 11. Total number of perching events at the top of perches at Sleepy Hole in 2013 for each species on short (30cm) and tall (90cm) perches.

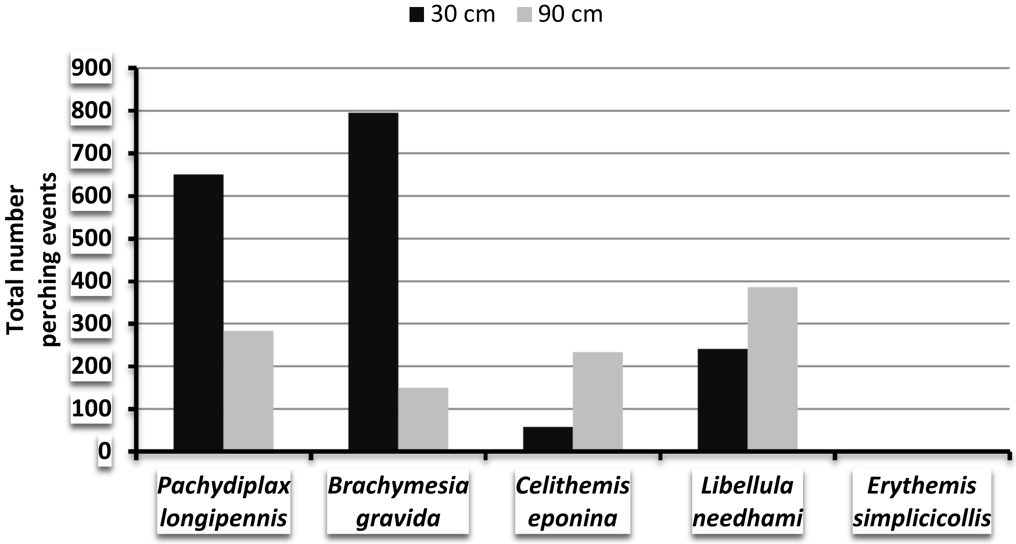

Figure 12. Total number of perching events at the top of perches at Hoffler Creek in 2011 for each species on short (30cm) and tall (90cm) perches.

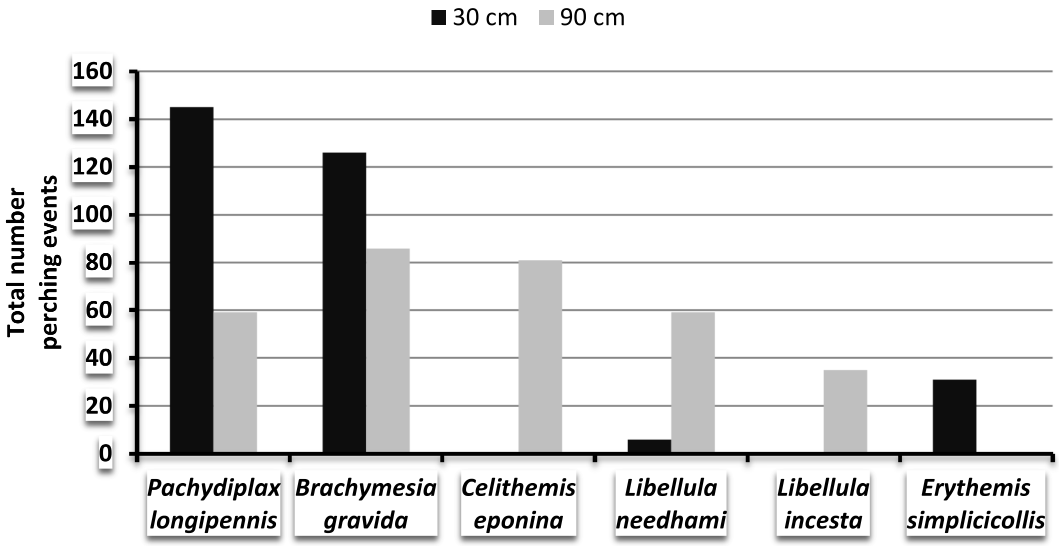

Figure 13. Total number of perching events at the top of perches at Hoffler Creek in 2012 for each species on short (30cm) and tall (90cm) perches.

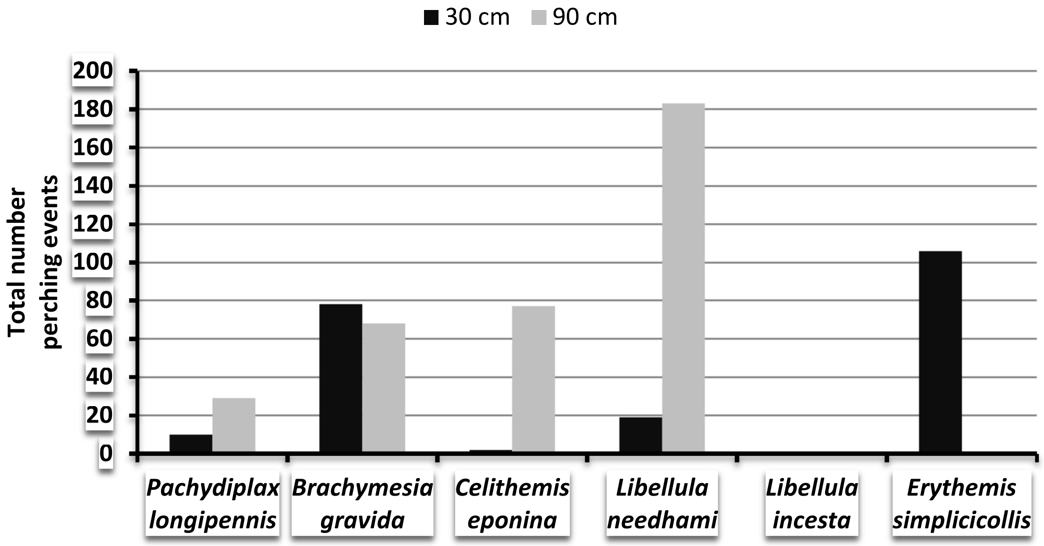

Figure 14. Total number of perching events at the top of perches at Hoffler Creek in 2013 for each species on short (30cm) and tall (90cm) perches.

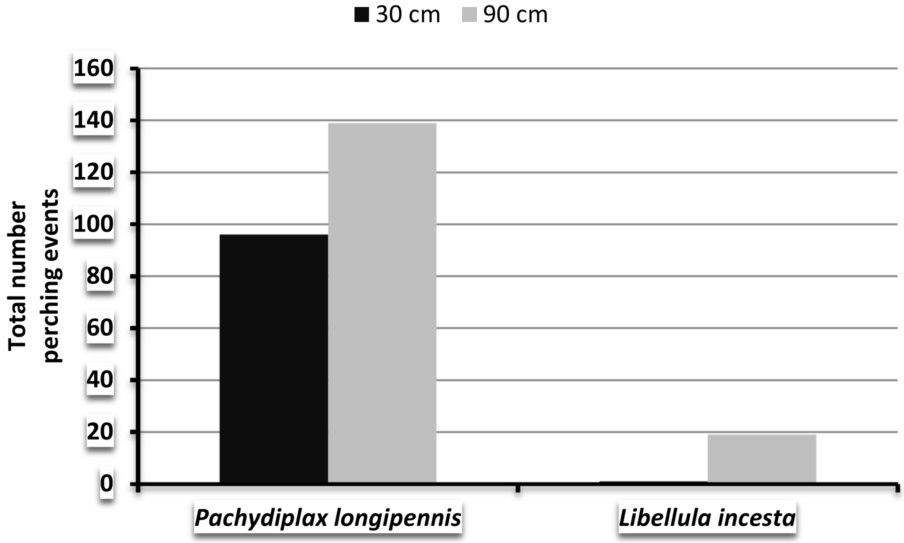

Figure 15. Total number of perching events at the top of perches at Lake Whitehurst in 2012 for each species on short (30cm) and tall (90cm) perches.

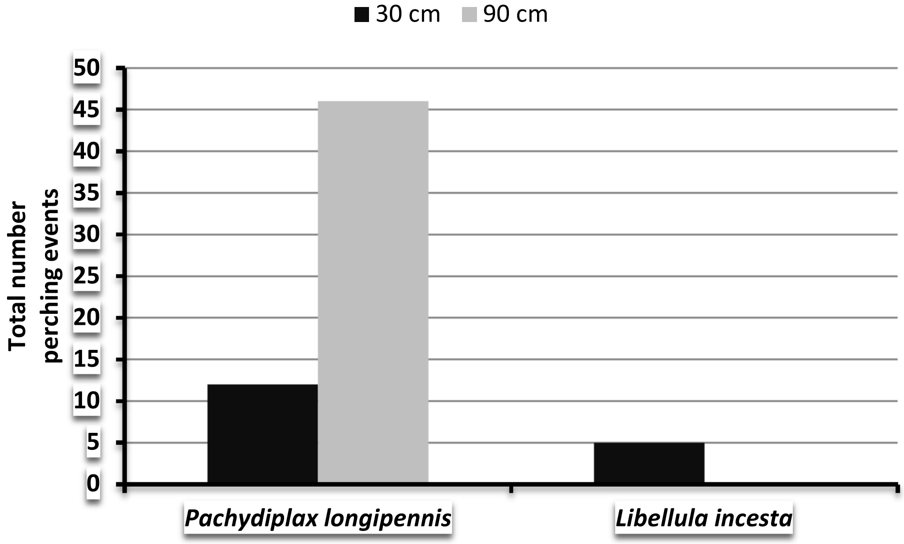

Figure 16. Total number of perching events at the top of perches at Lake Whitehurst in 2013 for each species on short (30cm) and tall (90cm) perches.

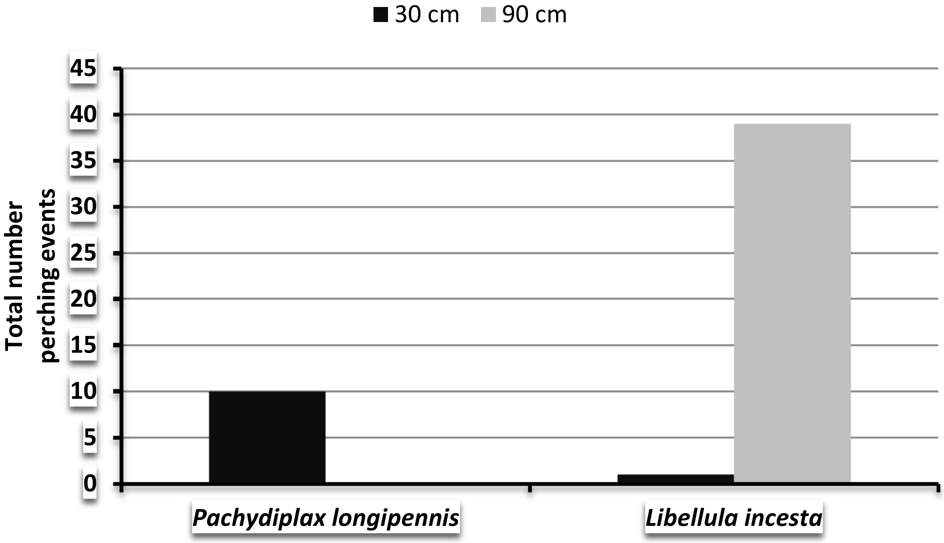

Figure 17. Total number of perching events at the top of perches at Stumpy Lake in 2012 for each species on short (30cm) and tall (90cm) perches.

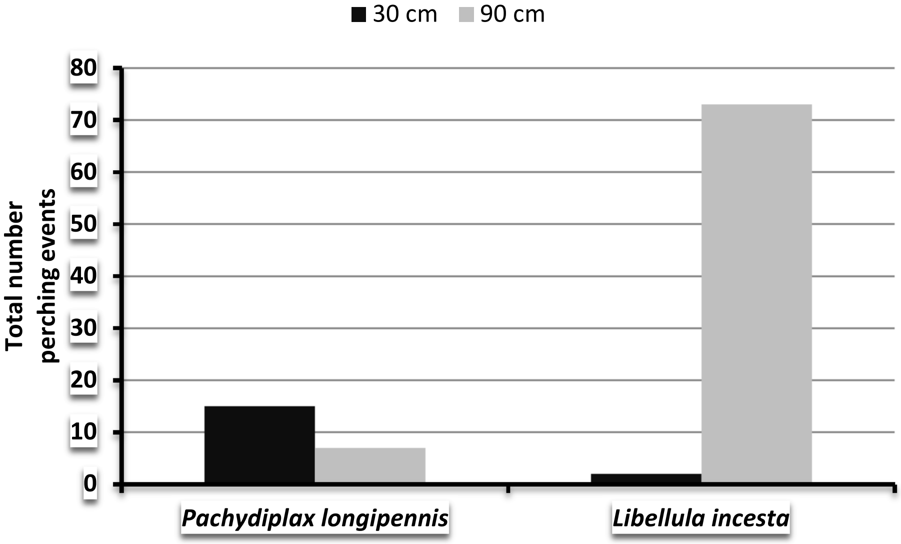

Figure 18. Total number of perching events at the top of perches at Stumpy Lake in 2013 for each species on short (30cm) and tall (90cm) perches.

Position on perch results

All six species that vied for perches at the study sites occasionally perched on the side of perches in addition to perching on the top (Figures 19-22). *Pachydiplax longipennis*, *Brachymesia gra*vida and *Celithemis eponina* perched on the side only a few times over the three years. In contrast, *Libellula needhami*, *L. incesta*, *Erythemis simplicicollis*, and *Perithemis tenera* often perched on the side (Figures 19-21). Male dragonflies frequently perched on the side of both occupied and unoccupied perches, but the majority of side perching events occurred on unoccupied perches at both Sleepy Hole (Table 8) and Hoffler Creek (Table 9). When another dragonfly perched on top, it was most likely to be a different species than the side percher. Most of the side perching events with another dragonfly on top were under *P. longipennis*, which probably occurred because *P. longipennis* perched on top so frequently at all the study sites. Side perching at Lake Whitehurst and Stumpy Lake always occurred on unoccupied perches, probably because the density of perching dragonflies was lower at those sites.

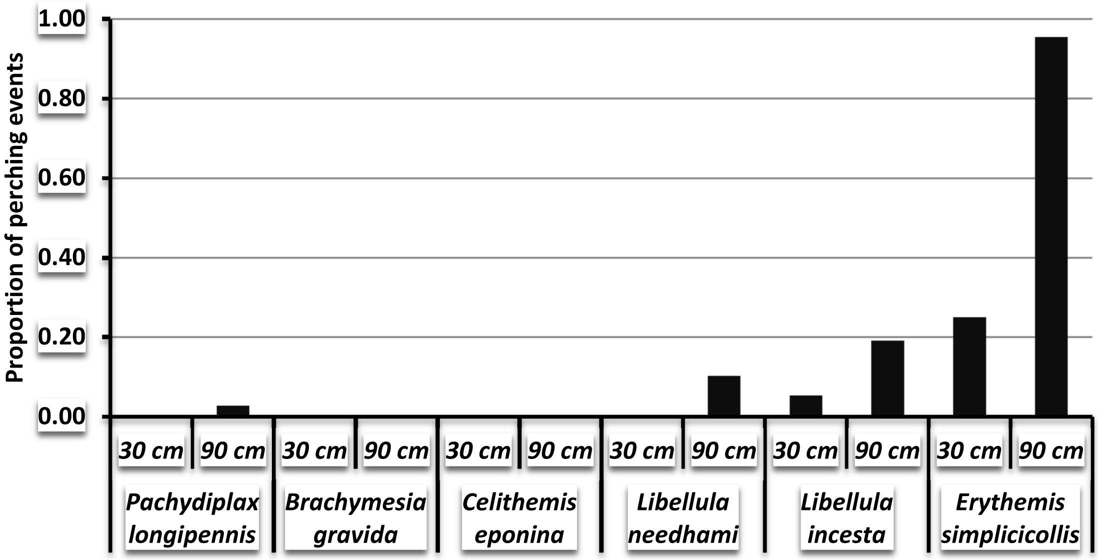

Figure 19. Proportion of perching events per species on the side of short (30cm) and tall (90cm) perches at Sleepy Hole 2012-013.

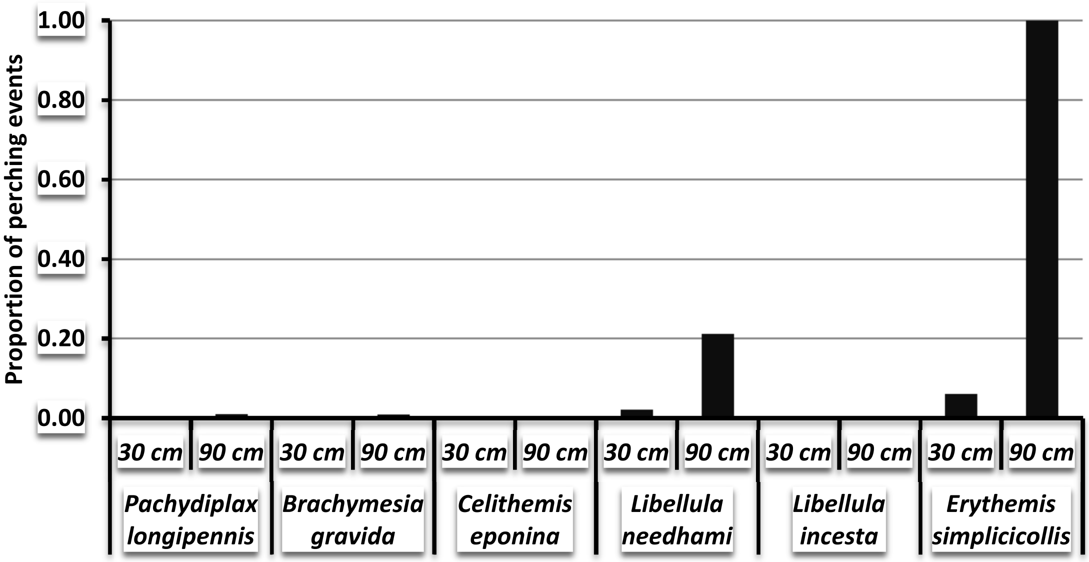

Figure 20. Proportion of perching events per species on the side of short (30cm) and tall (90cm) perches at Hoffler Creek 2011-2013.

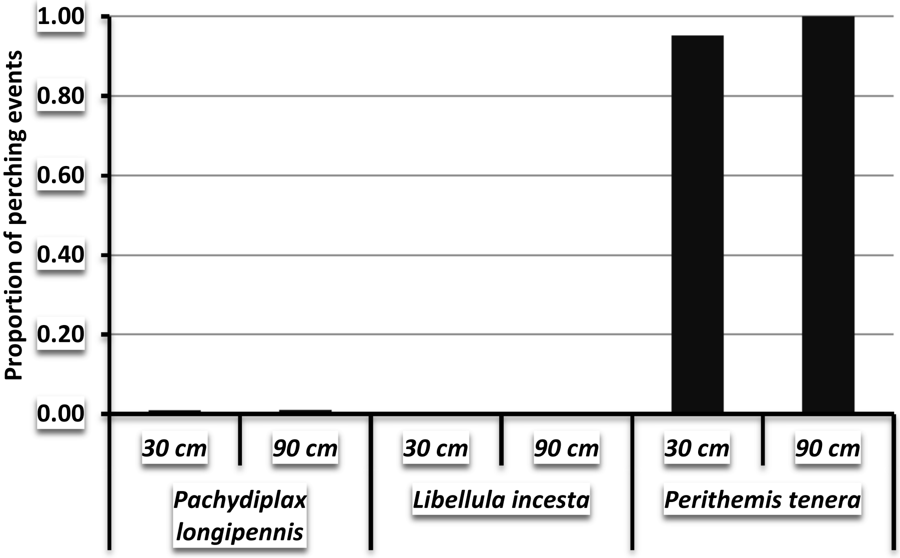

Figure 21. Proportion of perching events per species on the side of short (30cm) and tall (90cm) perches at Lake Whitehurst 2012-2013.

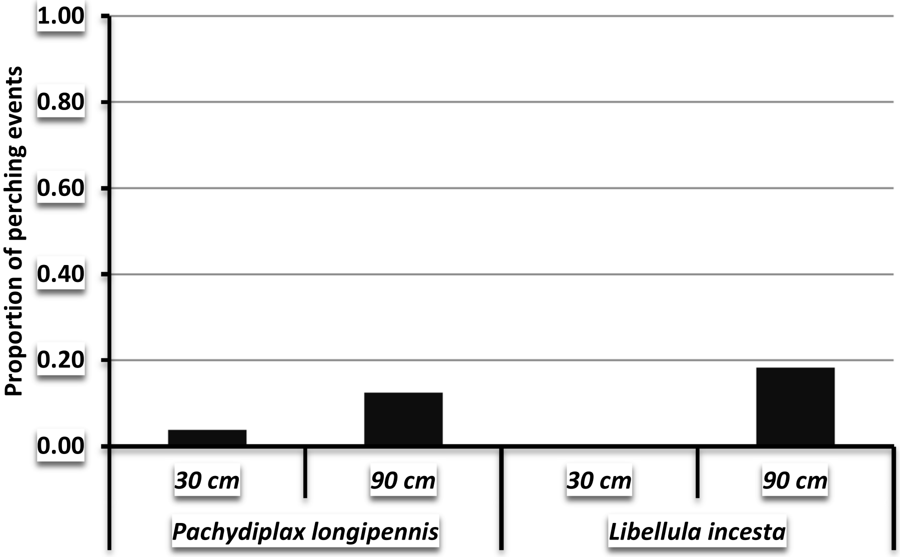

Figure 22. Proportion of perching events per species on the side of short (30cm) and tall (90cm) perches at Stumpy Lake 2012-2013.

Table 6. Number of times dragonflies perched on the sides of tall (T) or short (S) perches when another dragonfly or none was on top of the perch at Sleepy Hole 2012-2013. *Pachydiplax longipennis* (*Plo*), *Brachymesia gravida* (*Bg*), *Celithemis eponina* (*Ce*), *Libellula needhami* (*Ln*), *Libellula incesta* (*Li*), *Erythemis simplicicollis* (*Es*), *Perithemis tenera* (*Pt*), *Libellula luctuosa* (*Ll*), *Plathemis lydia* (*Ply*).

	Plo		*Bg*		*Ce*		*Ln*		*Li*		*Es*		*Pt*		*Ll*		*Ply*		Total
on top	T	S	T	S	T	S	T	S	T	S	T	S	T	S	T	S	T	S	
Plo	3						5		29		9	2			15				63
Bg	1								1										2
Ce																			
Ln																			
Li	14						4				2	2			1			1	24
Es																			
None	13				1		9		81	2	16	11			9			3	145
Total	31				1		18		111	2	27	15			25			4	234

Table 7. Number of times dragonflies perched on the sides of tall (T) or short (S) perches when another dragonfly or none was on top of the perch at Hoffler Creek 2011-2013. *Pachydiplax longipennis* (*Plo*), *Brachymesia gravida* (*Bg*), *Celithemis eponina* (*Ce*), *Libellula needhami* (*Ln*), *Libellula incesta* (*Li*), *Erythemis simplicicollis* (*Es*), *Perithemis tenera* (*Pt*), *Libellula luctuosa* (*Ll*), *Plathemis lydia* (*Ply*).

	Plo		*Bg*		*Ce*		*Ln*		*Li*		*Es*		*Pt*		*Ll*		*Ply*		Total
on top	T	S	T	S	T	S	T	S	T	S	T	S	T	S	T	S	T	S	
Plo					1		53	8			1	5							68
Bg	2	1		1			18					2							24
Ce							50												50
Ln	1						5				4								10
Li																			
Es																			
None	5	3		2	2		189	5			8	7							221
Total	8	4		3	3		315	13			13	14							373

Table 8. Number of times dragonflies perched on the sides of tall (T) or short (S) perches when another dragonfly or none was on top of the perch at Lake Whitehurst 2012-2013. *Pachydiplax longipennis* (*Plo*), *Brachymesia gravida* (*Bg*), *Celithemis eponina* (*Ce*), *Libellula needhami* (*Ln*), *Libellula incesta* (*Li*), *Erythemis simplicicollis* (*Es*), *Perithemis tenera* (*Pt*), *Libellula luctuosa* (*Ll*), *Plathemis lydia* (*Ply*).

	Plo		*Bg*		*Ce*		*Ln*		*Li*		*Es*		*Pt*		*Ll*		*Ply*		Total
on top	T	S	T	S	T	S	T	S	T	S	T	S	T	S	T	S	T	S	
Plo																			
Bg																			
Ce																			
Ln																			
Li																			
Es																			
None		2	1										1	16					20
Total		2	1										1	16					20

Table 9. Number of times dragonflies perched on the sides of tall (T) or short (S) perches when another dragonfly or none was on top of the perch at Stumpy Lake 2012-2013. *Pachydiplax longipennis* (*Plo*), *Brachymesia gravida* (*Bg*), *Celithemis eponina* (*Ce*), *Libellula needhami* (*Ln*), *Libellula incesta* (*Li*), *Erythemis simplicicollis* (*Es*), *Perithemis tenera* (*Pt*), *Libellula luctuosa* (*Ll*), *Plathemis lydia* (*Ply*), *Libellula vibrans* (*Lv*).

	Plo		*Bg*		*Ce*		*Ln*		*Li*		*Es*		*Pt*		*Ll*		*Ply*		*Lv*		Total
on top	T	S	T	S	T	S	T	S	T	S	T	S	T	S	T	S	T	S	T	S	
Plo																					
Bg																					
Ce																					
Ln																					
Li																					
Es																					
None		1							20	4				2	5	2			7		41
Total		1							20	4				2	5	2			7		41

Intraspecific and interspecific contests

There were many contests over perches at Sleepy Hole and Hoffler Creek sites for years 2012-2013, which included intraspecific and interspecific contests that were either won or lost. A win included both the successful overtaking of a perch from a resident individual and the ability to maintain a perch as a resident when contested by another individual. A loss occurred when a resident individual was overtaken from a perch or when an individual unsuccessfully tried to overtake a resident. Because interspecific contests for any one species involved the interactions with five other species, the total number of interspecific contests was divided by five when a direct comparison could be made to intraspecific contests.

At Sleepy Hole, *P. longipennis* was involved in the highest number of contests. It tended to lose more intraspecific contests and win more interspecific contests, but there was no statistical difference between winning or losing intraspecific or interspecific contests ($x^2= 0.07$, $P>0.05$). *Brachymesia gravida* showed a similar pattern, but there was also no significant difference between winning and losing each type of contest ($x^2= 3.22$, $P>0.05$). These differences were also not significant for *L. needhami* ($x^2= 0.22$, $P>0.05$), *L. incesta* ($x^2= 0.3$, $P>0.05$), *E. simplicicollis* ($x^2= 1.03$, $P>0.05$), or *C. eponina* ($x^2= 0.01$, $P>0.05$).

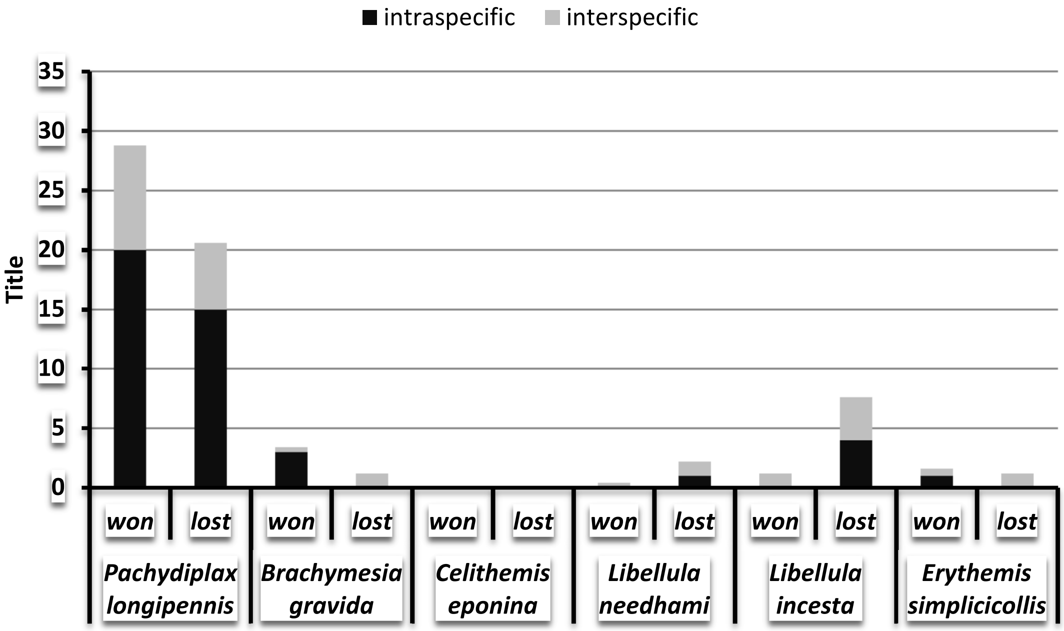

Figure 23. Number of intraspecific and interspecific wins and losses for each species at Sleepy Hole years 2012-2013. Interspecific numbers are averages based on total number of heterospecifics present.

At Hoffler Creek, *P. longipennis* tended to win more than it lost and had more intraspecific contests; however, there was no significant difference between winning or losing either type of contest (x^2= 5.23, P>0.05). Like Sleepy Hole, there were no significant differences for any of the species: *B. gravida* (x^2= 1.21, P>0.05), *C. eponina* (x^2= 1.95, P>0.05), *L. needhami* (x^2= 0.73, P>0.05), *L. incesta* (x^2= 0.01, P>0.05), *E. simplicicollis* (x^2= 2.73, P>0.05).

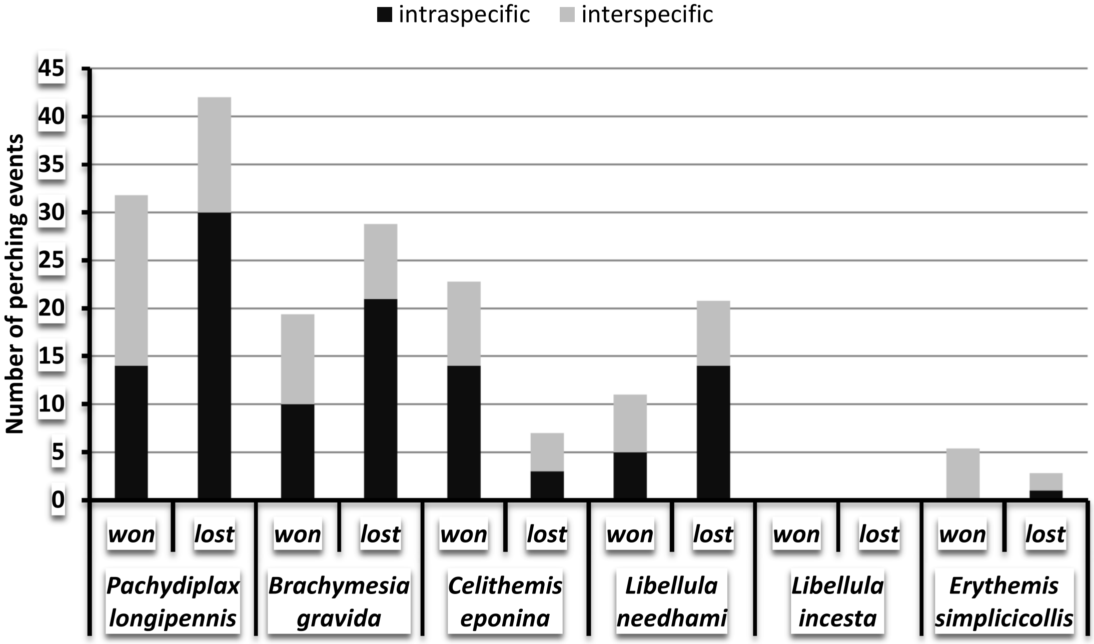

Figure 24. Number of intraspecific and interspecific wins and losses for each species at Hoffler Creek years 2011-2013. Interspecific numbers are averages based on total number of heterospecifics present.

Residency

The role of residency was examined by noting whether winners or losers were residents on the perch prior to the contest. Overall, there were more contests, both intraspecific and interspecific, at Hoffler Creek than at Sleepy Hole. *Pachydiplax longipennis* was involved in the most intraspecific and interspecific contests at both Sleepy Hole and Hoffler Creek for both years (Tables 6-7). *Brachymesia gravida*, *C. eponina*, *L. needhami*, and *E. simplicicollis* were involved in more contests at Hoffler Creek. *Libellula incesta* was the only species with more contests at Sleepy Hole than at Hoffler Creek.

As a resident, *P. longipennis* had the most interspecific contests with *B. gravida* and the second most contests with *L. needhami* at Hoffler Creek (Table 7). However at Sleepy Hole, *P. longipennis* had the most interspecific contests with *L. incesta* and the second most contests with *B. gravida* (Table 6).

At Hoffler Creek, *P. longipennis* won more contests as a resident than it lost against *B. gravida*, but at Sleepy Hole, the resident *P. longipennis* lost most of the contests to *B. gravida*. At Hoffler Creek, *B. gravida* won approximately the same number of contests as a resident as it lost to *P. longipennis* (22 wins versus 21 losses). At Sleepy Hole, the resident *B. gravida* lost more contests than it won against *P. longipennis*. Most of the contests between these species occurred on short perches. These two generalist species appeared to be evenly matched.

P. longipennis and *L. needhami* also appeared to be evenly matched. At Sleepy Hole, *P. longipennis* won and lost the same number of bouts as a resident against an intruder *L. needhami*. As a resident, *L. needhami* lost both of its contests against intruder *P. longipennis*. At Hoffler Creek, the resident *P. longipennis* won 23 and lost 20 bouts to *L. needhami* intruders, and the resident *L. needhami* won 20 and lost 18 bouts to *P. longipennis* intruders. All contests between these two species occurred on tall perches at Sleepy Hole and on both short and tall perches at Hoffler Creek.

At Sleepy Hole*, L. incesta* lost the majority of its contests as a resident against *P. longipennis* and *L. needhami* intruders, and it lost its only bout with a *B. gravida* intruder. As residents, *P. longipennis* won most of its bouts against *L. incesta* intruders, but *L.needhami* and *B. gravida* residents lost more bouts to *L.incesta* intruders. *L. incesta* appeared to be a poor competitor against *P, longipennis* but evenly matched with *L. needhami*.

At Hoffler Creek, *L. incesta* lost its only contest as a resident against a *P. longipennis* intruder. As an intruder at Hoffler Creek, *L. incesta* challenged only *B. gravida* where it won one and lost one contest, and it appeared to be evenly matched with this species.

Table 10. Total number of wins and losses by each resident species on short (30cm) and tall (90cm) perches at Sleepy Hole for years 2012-2013. Shaded boxes represent intraspecific contests. Intruder species are listed on the left column.

		RESIDENTS											
		P. longipennis		B. gravida		C. eponina		L. needhami		L. incesta		E. simplicicollis	
		won	lost	won	lost	won	lost	won	lost	won	lost	won	lost
P. longipennis	30cm	12	10	2	4	0	0	0	0	0	1	3	6
	90cm	8	5	0	1	0	0	0	2	2	5	0	0
B. gravida	30cm	1	8	3	0	0	0	0	0	0	0	0	0
	90cm	0	4	0	0	0	0	0	0	0	1	0	0
C. eponina	30cm	0	0	0	0	0	0	0	0	0	0	0	0
	90cm	3	0	0	0	0	0	0	0	0	0	0	0
L. needhami	30cm	0	0	0	0	0	0	0	0	0	0	0	0
	90cm	3	3	0	0	0	0	0	1	4	11	0	0
L. incesta	30cm	0	1	0	0	0	0	0	0	0	0	0	0
	90cm	37	7	0	1	0	0	2	4	0	4	0	0
E. simplicicollis	30cm	0	5	0	0	0	0	0	0	0	0	1	0
	90cm	0	0	0	0	0	0	0	0	0	0	0	0
TOTAL		64	43	5	6	0	0	2	7	6	22	4	6

Table 11. Total number of wins and losses by each resident species on short (30cm) and tall (90cm) perches at Hoffler Creek for years 2011-2013. Shaded boxes represent intraspecific contests. Intruder species are listed on the left column.

		RESIDENTS											
		P. longipennis		B. gravida		C. eponina		L. needhami		L. incesta		E. simplicicollis	
		won	lost	won	lost	won	lost	won	lost	won	lost	won	lost
P. longipennis	30cm	13	19	19	14	2	0	11	7	0	0	0	0
	90cm	1	11	3	7	11	5	9	11	0	1	0	0
B. gravida	30cm	41	24	4	13	3	1	4	6	0	0	23	9
	90cm	12	7	6	8	11	13	5	6	0	0	0	0
C. eponina	30cm	6	1	3	2	1	1	1	3	0	0	0	0
	90cm	7	8	7	8	13	2	0	1	0	0	0	0
L. needhami	30cm	10	8	7	3	3	0	1	9	0	0	4	0
	90cm	13	12	6	3	14	1	4	5	0	0	0	0
L. incesta	30cm	0	0	1	0	0	0	0	0	0	0	0	0
	90cm	0	0	0	1	0	0	0	0	0	0	0	0
E. simplicicollis	30cm	0	0	1	1	0	0	0	0	0	0	0	1
	90cm	0	0	0	0	0	0	0	0	0	0	0	0
TOTAL		103	90	57	60	58	23	35	48	0	1	27	10

Residents perched most often for less than one minute both winning and losing for *B. gravida*, *C. eponina*, *L. needhami*, *L. incesta* and *E. simplicicollis* at Sleepy Hole. However, *P. longipennis* won more times when perched for longer than one minute at Sleepy Hole. Resident odonates at Hoffler Creek also perched most often for less than one minute for both winning and losing for all species except *E. simplicicollis*, who won more often when perched for longer than one minute.

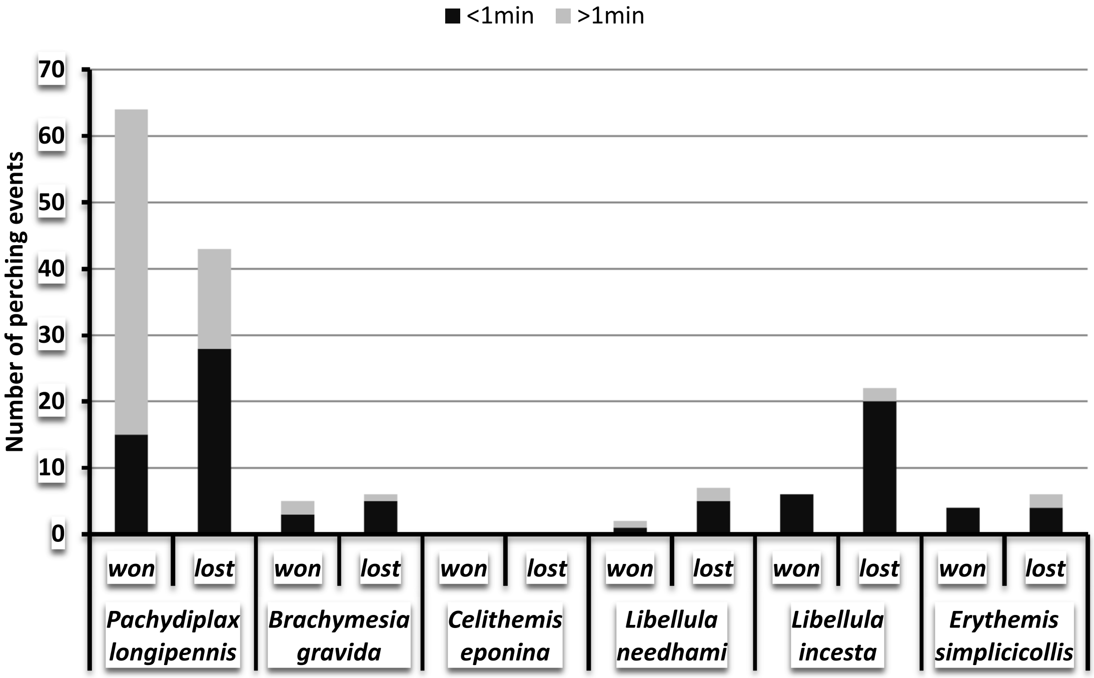

Figure 25. Perching times for residents either winning or losing contests at Sleepy Hole 2012-2013.

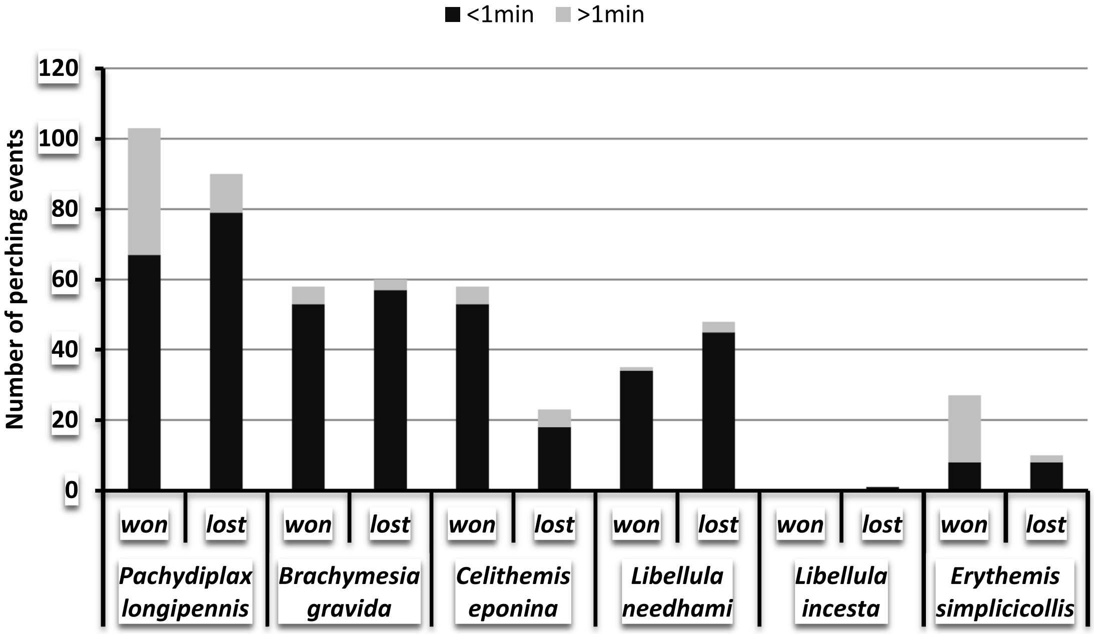

Figure 26. Perching times for residents either winning or losing contests at Hoffler Creek 2012-2013.

CHAPTER 4

DISCUSSION

Size parameters

Hypothesis 1 that species would vary in size was supported for all the parameters measured. In addition, sexual size dimorphism (SSD) was observed in some species for total length, cerci length, forewing and hindwing width and fresh mass.

Dragonfly species varied significantly in total body length. Results indicated that *Perithemis tenera* was the smallest species and *L. vibrans* was the largest species. For the other species, there were three main size classes: *P. longipennis* and *C. eponina* were small species, *E. simplicicollis* was a medium-sized species, and *B. gravida, L. needhami, and L. incesta* were large species. Bried et al. (2005) found that total body length is positively correlated with fresh mass in libellulid dragonflies. Bried and (2007) found body length is a better predictor than hind wing length for odonate dry mass.

Males of *P. tenera*, *P. longipennis* and *L. vibrans* were larger in total body length than females of those species. These three species are considered territorial (Serrano-Meneses 2008b) and therefore large male size conforms to expectations for SSD. In a review of odonate size, Serrano-Meneses et al. (2008b) found that *P. tenera* and *P. longipennis* are longer than females, but females of *L. vibrans* are longer than males. Large size may help male odonates secure better quality territories (Switzer, 2004; Serrano-Meneses et al., 2008a) and increase the chances of a male winning in intraspecific contests in high density populations (McCauly, 2010). In contrast, selection may favor large, fecund females, which may be more important than large male size in some species (Serrano-Meneses et al., 2008). In the other species in the present study, males and females did not differ significantly in body size. Similarly, Serrano-Meneses et al. (2008) noted that *C. eponina*, *L. needhami, and L. incesta* females were very slightly shorter than males.

Male cerci length varied significantly among species. *P. tenera* had the smallest cerci, and *P. longipennis C. eponina*, and *E. simplicicollis* had cerci of intermediate size.

The longest cerci were found in *B. gravida* , *L. needhami, L. incesta* and *L. vibrans.* Cerci length differences tended to reflect species differences in total length.

The cerci length was longer for males than females in *P. tenera*, *P. longipennis C. eponina*, *E. simplicicollis* and *L. vibrans*. There were no males collected of *Plathemis lydia*, and too few females of *L. needhami and L. incesta* measured to show significant gender differences in cerci length. Males use their cerci to grasp the female during copulation (Corbet, 1980; Cordoba-Aguilar et al., 2015) and therefore longer male cerci might be expected in most species. However, the two female *B. gravida* measured in this study had longer average cerci length than did the ten males. More research on the reproductive biology of this species is warranted in order to understand this difference.

Male forewing and hindwing lengths varied significantly among species and followed a similar pattern. Both forewings and hindwings were shortest in *P. tenera* and longest in *L. vibrans*. Wing length is relatively longer in Libellulidae dragonflies than in other families (Sacchi and Hardersen 2013), and typically migratory species have longer wings than nonmigratory species. However, none of the species in the present study were considered migratory (Sacchi and Hardersen 2013). Van Buskirk (1987) found that hind wing length is significantly correlated with both head width and dry weight in *Sympetrum rubicundulm*. McCauly (2013) suggested wing size is related to dispersal ability in *L.incesta*, which has smaller wings and lower dispersal rates and distances than its congeners, *L. pulchella* and *L. luctuosa.* In the present study, *L. incesta* fore and hindwings differed significantly from its congeners. Wing lengths were significantly longer for *L. incesta than L. needhami* and significantly shorter than *L. vibrans*. Fore and hindwing widths were similar for *L. incesta* and *L. needhami*, but significantly wider for *L. vibrans*. Both *L. needhami* and *L. vibrans* occurred at three of the study sites but were not observed at Lake Whitehurst. *L. incesta* was sighted at all four study sites, but was not common at Hoffler Creek. It is unclear whether or not *L. incesta* differs in dispersal ability from its congeners in southeastern Virginia.

There were no gender differences for forewing or hindwing lengths. In contrast, Wong-Munoz et al. (2011) found that male *Pachydiplax longipennis* have significantly longer wings than do females.

Both male forewing and hindwing widths varied significantly among species and followed a similar pattern. *P. tenera* had the narrowest forewings and hindwings. The forewings and hindwings of *P. longipennis* and *E. simplicicollis* were wider than those of *P. tenera* but narrower than those of *C. eponina*, *B. gravida*, *L. needhami, and L. incesta*. *L. vibrans* had the widest forewings and hindwings.

Wing shape is variable in Odonata and reflects habitat use, mate-guarding behavior and migratory ability (Johansson et al., 2009). In general, broader wings are found in species that frequent open habitats and mate-guard in tandem. Migrating species have lobes at the base of the fore wing and hind wing. Outomuro et al (2013) noted that species with colored wings tend to have a broader wing base, which is probably related to sexual selection. They also noted that female hindwing shape is significantly related to both landscape type and wing coloration. Broad, brightly colored wings are characteristic of both male and female *C. eponina* which mate-guard in tandem.

In this study, both forewing and hindwing widths of females were larger than males for *P. tenera*, *P. longipennis* and *B. gravida*, and forewings but not hindwings were wider for female *E. simplicicollis*. Wider wings are associated with gliding behavior, which conserves energy (Johansson et al., 2009). Male wings may be selected to be narrower due to the increased agility needed to actively defend territories against other males. Females fly only to forage and locate mates and oviposition sites, and energy conservation may be a high priority for them.

Male fresh mass varied significantly among species. *P. tenera* had the lowest mass; *P. longipennis, C. eponina, E. simplicicollis* weighed more than *P. tenera*, but less than *B. gravida*. The next heaviest species were *L. needhami* and *L. incesta* which both weighed less than *L. vibrans*.

While most species showed no gender differences in fresh mass, two species, *E. simplicicollis* and *L. vibrans* had females that were heavier than males. Similarly, Bried et al. (2005) found that the fresh mass of female *E. simplicicollis* was greater than that of males. They also noted that *L. vibrans* females tended to be larger than males but the difference was not significant. These gender differences may have resulted if the females had mature eggs waiting to be fertilized. Frequently, females would release unfertilized eggs during measurements in the present study. Both males and females increase in mass from emergence to maturity (Marden, 1989; Anholt et al., 1991), and gender differences may have been due to differences in age of the capture specimens. Similar to the present study, Bried et al. (2005) found that *P. tenera* and *P. longipennis* males and females did not differ in fresh mass. In contrast, they noted that *C. eponina* males have significantly greater fresh mass than females, but male and female *C. eponina* did not differ in fresh mass in the present study.

Overall, the recapture rate was low (0.01 and 0.05 for 2013 and 2014, respectively). This may indicate low site fidelity and high mobility due to foraging (Baird & May, 1997). Marked dragonflies generally disappeared from the area. In contrast, in a study of *Macrothemis imitans*, marked males went back to their territories following capture (Mourao & Peixoto, 2014). In another study, over 40% of *Libellula depressa* were recaptured by viewing marked individuals through binoculars (Angelibert & Giani, 2003). In a study of *Tanypteryx hageni*, Clement and Meyer (1980) recaptured seven of 22 marked dragonflies, including one caught five weeks after marking. Johnson (1962) found that fifteen marked *Pachydiplax longipennis* remained in the area from 10 minutes to three hours. In a study of *Plathemis lydia*, Jacobs (1955) found marked males returned to the site for 8-14 days and females returned for 13-24 days.

Perch height

Hypothesis 2 that perch height is related to dragonfly size was not supported. Larger dragonflies did not always select the tops of taller perches. *Pachydiplax longipennis*, a small species, was a generalist of perch height selection and perched on both tall and short artificial perches at all four sites. This species is known to be generalist in feeding habits (Baird & May, 1997), overall behaviors (Baird & May, 2003) and antipredator behavior as nymphs (Hopper, 2001). *Brachymesia gravida,* a large species, also perched on both tall and short perches at both Sleepy Hole and Hoffler Creek.

Celithemis eponina, a small species, perched primarily on tall perches at both Sleepy Hole and Hoffler Creek. This species is considered non-territorial by Serrano-Meneses et al. (2008b), and perching in the present study may have been related to mating behavior because this species was observed in tandem throughout the season.

Erythemis simplicicollis, a medium-sized territorial species (Serrano-Meneses et al., 2008b) perched almost exclusively on short perches at both Sleepy Hole and Hoffler Creek. *Erythemis simplicicollis* typically perches and mates very low on perches or on floating vegetation (Robey, 1975; Baird & May, 2003; personal observations). These two species are known to contradict the size-dependent hypothesis of perch height selection (Worthen & Jones, 2007; Worthen & Phillips, 2014).

Libellula needhami, a large species, perched most often on the tall perches at Sleepy Hole and Hoffler Creek. *Libellula incesta*, another large species, perched primarily on the tall perches at Sleepy Holes, Hoffler Creek and Stumpy Lake. The few times it perched at Lake Whitehurst, it selected tall perches in 2012 and short perches in 2013.

Position on perch

Hypothesis 3 that species position on perches is related to size with the larger dragonflies perching on top was not supported. However, the related hypothesis that perch position is related to competitive ability appears to be supported. While most species perched on the side of the perch at least once, *L. needhami* and *E. simplicicollis* perched most often on the sides of the perches at Sleepy Hole and Hoffler Creek. *Libellula incesta* perched on the side almost 20% of the time at both Sleepy Hole and Stumpy Lake. *Perithemis tenera* perched almost exclusively on the side of perches at Lake Whitehurst. Therefore dragonflies perching on the side ranged in size from very small to medium to large. Males in this study also received almost no antagonistic encounters by other individuals when perched in this manner, and there never seemed to be competition for side perch positions. The four species that perched on the side most frequently (*L. needhami, E. simplicicollis*, *L. incesta* and *P. tenera*) tended to be poor competitors who lost more than they won of their intra- and interspecific contests. The species that engaged in the most competitions, *P. longipennis*, only rarely perched on the sides of perches. Pezalla (1979) found *Libellula pulchella* position on the perch is related to maximizing or minimizing sun exposure. These dragonflies perch at the top of perches, but sometimes position themselves parallel to the perch either directly exposed to the sun's rays or on the other side of the perch (Pezalla, 1979).

In the present study, *P. tenera* rarely selected the artificial bamboo perches and then perched only on the side of the perch at one study site. It was not involved in intra- or interspecific contests in this study. Switzer and Eason (2003) found 43 out of 50 *P. tenera* individuals perched on the side of their territories. They also found that residents that perched on the territory sides had lower numbers of intrusions from other males than residents perched in the middle or on the other side of the territory (Switzer & Eason 2003). Neighbor intrusions were more important in determining where males perched than were visits to the territory by females.

Intraspecific and interspecific contests

Hypothesis 4 that there would be more intraspecific than interspecific contests was not supported when the number of contests was corrected for total number of species involved in interspecific contests. There was no significant difference between intra- or interspecific contests for any of the species. These results differ from numerous studies focusing on communities of dragonflies that have found more intraspecific contests (Lutz & Pittman, 1970; Baird & May, 2003; Worthen & Patrick, 2004).

In a study of *Leucorrhina frigida*, *L. proxima* and *L. intacts*, Singer (1989) found *L. frigida* and *L. intacta* aggressively chase both heterospecific and conspecific intruders with equal frequency, but *L. proxima* primarily chases conspecifics. Curry and Kennedy (2010) found that *Plathemis lydia* chases heterospecific perching species from its territory approximately every other minute.

Body size differences have been found to affect interspecific contest outcomes and facilitate niche partitioning in the use of different perch heights (Worthen & Jones, 2007). Kasuya et al. (1997) found that territorial males of *Orthetrum japonicum* are larger in body width than intruders; however, residents win most contests regardless of differences in body size. Body size did not influence contest outcomes in the present study, and the small species *P. longipennis* was by far the best competitor in the community.

Residency on a perch might influence contest outcomes. Mourao and Peixoto (2014) noted that resident males of *Macrothemis imitans* win 100% of contests over perches. Also, if the resident is removed by the experimenters and a substitute male takes over the perch, the substitute residents also win 100% of the contests. Residents and substitutes did not differ in dry mass, wing area, thoracic muscle mass or fat content (Mourao and Peixoto, 2014). In *Perithemis tenera*, residents win contests that are not escalated, but if contests are escalated, younger males generally win (Switzer, 2004). Resident males of *Sympetrum rubicundulum* win more contests (Van Buskirk, 1986). Resident *Tanypteryx hageni* males win every encounter with heterospecific intruders (Clement and Meyer 1980). Resident males also win every intraspecific contest, which outnumbered the interspecific contests. Johnson (1962) noted that *Pachydiplax longipennis* male residents tended to win more contests, but the sample size was small.

Moore (1987) found that as *Libellula luctuosa* density increased, males perch less and chase intruders more frequently. The same pattern was observed in *Pachydiplax longipennis* (Fried and May, 1983). Sherman (1983) found that at high density, resident *P. longipennis* males are more likely than non-resident males to secure mates. Kasuya et al. (1997) found that territorial males of *Orthetrum japonicum* are larger in body width than intruders, however, residents win most contests regardless of differences in body size.

In the present study, residency did not guarantee a contest win and in fact *B. gravida*, *L. needhami* and *L. incesta* lost more contests as residents than they won at both Hoffler Creek and Sleepy Hole. *Pachydiplax longipennis*, *C. eponina* and *E. simplicicollis* won a few more contests as residents than they lost at Hoffler Creek, but E. *simplicicollis* lost more than it won as a resident at Sleepy Hole. Length of time a male held a perch as a resident did not affect the contest outcome. Only two species, *P. longipennis* at Sleepy Hole and *E. simplicicollis* at Hoffler Creek, won more contents when they resided on the perch for longer than a minute. The majority of residency times for both winners and losers was less than a minute.

CHAPTER 5

CONCLUSION

Overall, the results of this study revealed that dragonfly communities varied from site to site, even when many of the same species were present. The species varied widely in size as measured by total length, abdomen length, cerci length, fore and hindwing lengths and fresh mass. Gender differences were species specific for most parameters. For most species, females had greater fore and hindwing widths than males, and this difference may be related to differential habitat use and energy conservation strategies. Males of the generalist species *P. longipennis* and *B. gravida* were flexible in perch height selection and engaged in many intra- and interspecific contests over perch possession. More specialist species tended to select either tall (*C. eponina*, *L. needhami* and *L. incesta*) or short (*E. simplicicollis*) perches, and these choices were not related to dragonfly size. Perching on the sides of perches has not been reported widely in the literature. In fact, the species that engaged in this practice most frequently in this study, *L. needhami*, has received very little attention from researchers since its description (Westfall, 1943). This large dragonfly appeared to be a poor competitor, and this may explain its side perching behavior. Size also played no role in interspecific contest outcomes for any species. Some species such as *C. eponina*, *L. needhami* and *L. incesta* engaged in more contests at one site than the other. This observation may be responsible for the designation of *C. eponina* as non-territorial (Serrano-Meneses et al. 2008b). In the present study, this species engaged in numerous contests at Hoffler Creek and none at all at Sleepy Hole. Therefore it is valuable to examine the behavior of a given species in a number of sites before drawing conclusions about territoriality. Although many studies have indicated that length of residency on a perch influences contest outcomes, residency was not important in determining winners or losers in this study. In fact, most males remained on a perch for less than a minute and most left voluntarily. Robey (1975) also found that *Pachydiplax longipennis* leaves its perch every 10-20 seconds.

In the present study, dragonfly size and residency on a perch were not important in determining contest winners or losers, and bouts with heterospecifics were as frequent as with conspecifics. These findings contribute to the growing body of literature that dragonfly community interactions are dynamic and do not follow simple rules.

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