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Confirming the relationship between body size and perch height in tropical odonates (Odonata: Libellulidae): wet-season contrasts and experimental tests

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In a previous study conducted during the dry season at La Selva Biological Station, Costa Rica, mean perch height of libellulid dragonfly species (Odonata: Libellulidae) correlated with male body size, and interactions between species suggested a size-dependent competitive hierarchy. Here, I report on a wet-season study that examined whether seasonal changes in community composition affect these patterns. Males were captured, photographed, and marked, perch heights among individuals and species on natural and artificial perches (25, 50, and 100 cm) were compared, and the frequencies of aggressive interactions between species were analyzed. I also examined the responses of *Micrathyria atra* and *Micrathyria mengeri* males to decoys of these species placed in their territory at different heights (50 or 100 cm). Although the wet season community differed from the dry season community (Jaccard dissimilarity = 0.778), there was still a significant correlation between species perch height and body size, on both natural and artificial perches. Interspecific interactions supported the size-dependent competitive hierarchy hypothesis: smaller species that perched low avoided attacks by larger species. These patterns were confirmed in the decoy experiment. The larger *M. atra*, which perches at ∼100 cm, attacked decoys at 100 cm almost exclusively, and attacked decoys of the smaller *M. mengeri* more than conspecifics. In contrast, *M. mengeri* (which perches at 50 cm) only attacked decoys placed at 50 cm. Although community membership changed, the correlation between body size and perch height was maintained by a size-dependent competitive hierarchy in both dry and rainy seasons.

Keywords: dragonfly; community ecology; niche partitioning; perch selection; seasonality

Introduction

Seasonal change in the composition of tropical odonate communities is not well studied (Renner, Sahlén, & Périco, 2016). Although temperatures are favorable throughout the year and some species have year-long flight seasons (Koparde, 2016), many tropical odonates have only one generation a year (Corbet, 1999, pp. 218–220). Adult emergence of these species, and even multivoltine species (Reels, 2011), usually correlates with the onset or abatement of the rainy season (Dudgeon, 1989a, 1989b; Kulkarni & Subramanian, 2013; Kumar, 1972, 1976, 1985; Pritchard, 1996) and usually contributes to greater dragonfly diversity during these periods (Renner et al., 2016; Vilela, Ferriera, & Del-Claro, 2016). Activity patterns can also change seasonally. During the dry season, diurnal temperature changes dramatically and many species

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are only active during warm mid-day periods; in the rainy season, diurnal temperature is more stable and species are active for longer periods each day (De Marco & Resende, 2002).

Seasonal changes in community composition and species' activity patterns could cause changes in interspecific interactions and patterns of resource use (De Marco & Resende, 2004). Early species may gain important priority effects over later species in both larval and adult stages. Changes in arrival time can alter size relationships among larvae, change the direction of size-dependent intraguild predation between species, and affect community composition (Rasmussen, Van Allen, & Rudolph, 2014). In addition, adults that emerge early may be able to acquire territories and, as residents, hold these territories against conspecifics and heterospecifics alike (Parr, 1983; Resende, 2010; Suhonen, Rantala, & Honkavaara, 2008; Switzer, 2004).

Perch selection by territorial libellulids might be sensitive to seasonal changes in both community composition and species-specific activity patterns. Seasonal changes in the abundance or activity of competitively dominant species might change the abundance or behavior of competitive subordinates. During the dry season (January–February) of 2016, I conducted an observational study of perch height by male libellulids at La Selva Biological Station, Heredia Province, Costa Rica (Worthen, 2017). There was a significant correlation between species' mean perch height and body size, and patterns of aggression between the most abundant species were consistent with a size-dependent competitive hierarchy (Worthen, 2017). In addition, some species perched on particular substrates; for instance, *Erythrodiplax fervida* perches on grasses almost exclusively (Worthen, 2017). That study was conducted in a reserve where collecting and experimentation were not allowed. As such, individuals were not marked and mean perch heights of species were calculated on pseudoreplicated observations of an unknown number of individuals (Worthen & Hoke, 2018). In addition, the confounding relationship between substrate and perch height could not be addressed. In the present investigation, I conducted an observational and experimental study in a neighboring wetland during the wet season at La Selva, to see if there were seasonal changes in community composition, perch height selection, or interspecific interactions. By marking individuals, observing perching on natural and artificial perches, and placing live decoys into the territories of other males, I addressed the following questions: (1) does mean male body size of a species correlate with mean perch height in this wet season community; (2) does pseudoreplication of individuals affect this relationship; (3) do species use artificial perches in the same way as natural perches, or is substrate (and not height) important for perch selection; and (4) do territorial males attack invaders in a manner consistent with a size-dependent hierarchy?

Methods and materials

This research was conducted from 6–16 June 2017, along the Teska Elevated Boardwalk in the Research Wetland at La Selva Biological Station of the Organization for Tropical Studies (OTS), in Heredia Province, Costa Rica (10.43248 N, 84.008070 W). The boardwalk is 65 m long and bisects the wetland, which is approximately 100 m × 80 m. I established six perching stations in shallow (20–50 cm) open-water pools 2–5 m from the boardwalk, with approximately 10 m between each perching station. At each station, three wooden dowels (diameter = 7.5 mm) were stuck in the sediment to create artificial perches rising 25, 50, and 100 cm above the waterline. The sticks were placed 20 cm apart, with heights arranged in random order.

During rainless periods, I slowly walked the boardwalk and completed a transect every 30–45 min from 0730 to 1530 hours. I measured the perch height of male libellulids perching on natural vegetation, noting the species and perch height. I attempted to captured them by aerial net; those captured were marked with a unique identification (ID) number on one wing with a

Sharpie© felt-tipped marker, photographed for later size measurements (using ImageJ software; Rasband, 2018) and species confirmation using Paulson (2015), and released. In subsequent observations of these individuals on natural or artificial perches, their number was also recorded. If there was a dragonfly perched at a station, I observed that station for 10 min and recorded every perch event – recording the species, sex, perch height, and ID (if present). Females only 'perched' at a station when in tandem with a male, and these events were not included in these analyses. While observing a station, I also recorded interactions between dragonflies. I recorded a 'chase' if a perched dragonfly left the perch to chase another dragonfly, and an 'attack' if a perched dragonfly was attacked by another dragonfly. The species (and ID, if present) were recorded for each interaction.

To test the hypothesis that species perch at different heights, I compared mean male perch heights among species, on natural vegetation, in two ANOVA tests. In the first analysis, I conducted a nested ANOVA evaluating the differences among species based on the variation in mean perch height among marked individuals within species. This is a conservative test and only included the six species with at least two observations on each of two individuals (replication at the individual and species levels). In the second analysis, I pooled all observations of marked and unmarked males in a species, and compared all nine species observed at least twice. I compared the results of these analyses to assess the significance of within-species variation on between-species comparisons (Worthen & Hoke, 2018).

To test the hypothesis that species used the artificial perches in the same manner as natural perches, I compared the frequencies with which each species used the three artificial perch heights, using chi-squared tests of independence. I analyzed patterns in the complete dataset (including all nine species that perched at the stations), and among the four most common species ($N > 20$). For these comparisons, all perches made by males in a species (both marked and unmarked individuals) were pooled. To compare results on artificial and natural perches, I correlated species mean perch height on natural perches with mean perch height on artificial perches.

I tested the hypothesis that species mean perch height is positively correlated with body size using one-tailed Pearson correlations. I correlated mean forewing length of netted individuals with: (1) mean perch height of species on natural perches, calculated on mean height of marked individuals; (2) mean perch height of species on natural perches using all observations (all perches by marked and unmarked individuals pooled); and (3) mean perch height of species on artificial perches (individuals pooled).

I used two approaches to test the hypothesis that interspecific patterns in perch-height selection were a function of size-dependent interspecific aggression. First, I compared the frequencies of intra- and interspecific interactions among the four most common species using chi-squared goodness of fit tests. Expected values were generated from the proportional representation of species in the environment (as measured by the relative frequency of all observed perch events by these species, summed across natural and artificial perches). In other words, I tested the null hypotheses that these species interacted with one another at random, at rates equal to the relative abundance of these species in the habitat.

Second, I conducted an experiment that tested the hypothesis that aggressive interactions by perched *Micrathyria atra* (Martin) and *Micrathyria mengeri* Ris depend on the species and perch height of intruding males. I carefully taped the legs of a live male decoy to an artificial perch, and placed the decoy 2 m away from males perched at a station. Decoys were placed on either 50 cm or 100 cm perches, and were observed for 5 min intervals. Individual decoys were used for two or three trials, and then were carefully removed from the dowel and released (all but one decoy survived). Thirty trials were conducted with territorial *M. atra* males; 19 trials used *M. atra* decoys (nine replicates at 50 cm, 10 at 100 cm) and 11 trials used *M. mengeri* decoys (six replicates at 50 cm; five at 100 cm). Twenty trials were conducted with territorial *M. mengeri* males; 11 trials used *M. atra* decoys (four replicates at 50 cm; seven at 100 cm) and nine trials used *M. mengeri* decoys (seven replicates at 50 cm; two at 100 cm). The number of the attacks made by the territorial males were recorded, pooled, and compared with chi-square tests that corrected for differences in sample sizes. SPSS statistical software (IBM Corp., 2012) was used for all statistical analyses.

Results

On both natural and artificial perches, there were significant differences between species in male perch height. On natural perches, there were significant differences between species when individual variation among marked individuals was accounted for (marked individuals only, ‘Species’ effect, nested ANOVA, $F = 14.829$, $df = 5, 56$, $p < 0.001$), and when all observations (of marked and unmarked males) were pooled within species (‘Species’ effect, ANOVA, $F = 77.655$, $df = 9, 838$, $p < 0.001$). When species were compared based on individual mean perch heights, *Erythemis haematogastra* (Burmeister) and *Micrathyria atra* perched significantly higher than *M. mengeri*, *Nephepeltia phryne* (Perty), and *Micrathyria pseudeximia* Westfall (Tukey mean comparison tests, $p = 0.05$, Figure 1). A *Perithemis* species was intermediate to (and not significantly different than) *M. atra* and *M. mengeri* (Figure 1). This species is common around La Selva but still undescribed (*Perithemis* n. sp., Wagner, Paulson, Naskrecki, Esquivel, & Ramirez, 2000; W. Haber, pers. comm.); I will refer to it as ‘*Perithemis*’ henceforward. When all species were compared using pooled observations, the patterns among the six ‘core’ species were preserved ($r = 0.995$, $df = 5$, $p < 0.001$), *Libellula herculea* Karsch and *Cannaphila insularis* Kirby perched significantly higher than other species, and *Orthemis cultriformis* Calvert and *Dythemis nigra* Martin perched at heights similar to *Erythemis haematogastra* and *M. atra* (Tukey mean comparison tests, $p = 0.05$, Figure 2).

Males of nine species used the artificial perches, and were distributed across the three perch heights at significantly different frequencies ($\chi^2 = 333.413$, $df = 16$, $p < 0.001$; Table 1). *Cannaphila insularis* and *D. nigra* used only tall (100 cm) perches, *E. haematogastra*, *M. atra*, *O. cultriformis*, and *Perithemis* used tall and medium (50 cm) perches, and *M. mengeri*, *M. pseudeximia*, and *N. phryne* used all three heights (Table 1). However, since 55% of the cells have an expected value < 5 (which compromises the integrity of chi-square tests), I also analyzed patterns among the four most common species ($N > 20$): *M. atra*, *M. mengeri*, *N. phryne*, and

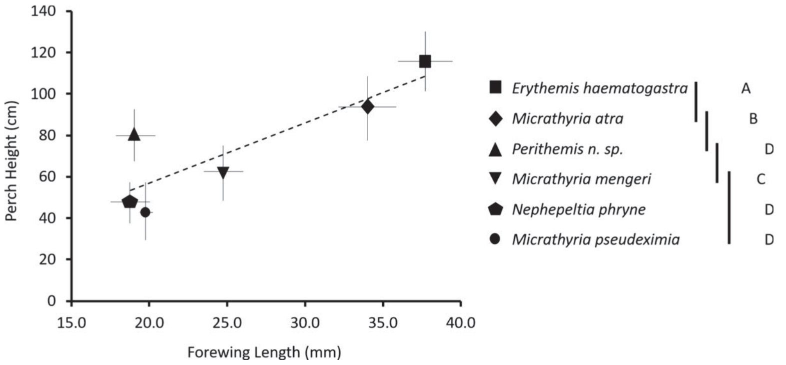

Figure 1. The significant relationship ($r = 0.817$, $df = 5$, $p = 0.015$) between mean (± 1 SD) male perch height (cm) of six libellulid species, based on mean perch heights of individuals on natural perches, and mean (± 1 SD) forewing length (cm), and a comparison of these means. Species connected by a line do not differ with respect to mean perch height; species followed by the same letter do not differ with respect to mean forewing length (Tukey mean comparison tests, $p = 0.05$).

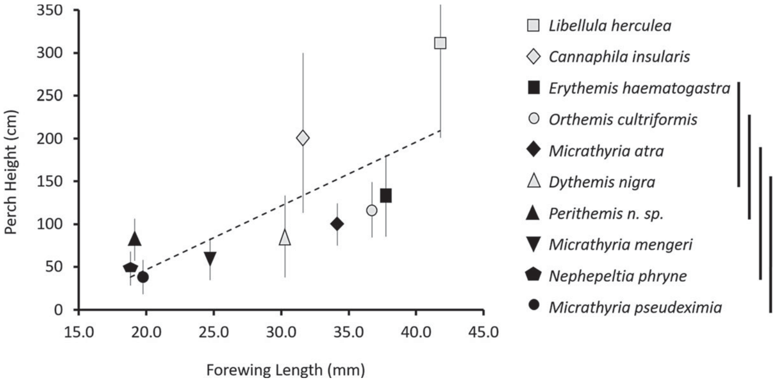

Figure 2. The significant relationship (r = 0.753, df = 9, $p = 0.006$) between mean (± 1 SD) male perch height (cm) of 10 libellulid species, based on pooled perch heights of species on natural perches, and mean (± 1 SD) forewing length (cm), and a comparison of mean perch heights (species connected by a line do not differ with respect to mean perch height; Tukey mean comparison tests, $p = 0.05$).

Table 1. The distributions of perch events by males of nine dragonfly species across artificial perches of three perch heights (25, 50, 100 cm above the water line), ordered by mean perch height. The distributions across all species, and the subset of common species (bold), were significantly different (see text for statistical comparisons).

	Perch height (cm)			
Species	25	50	100	Mean
Cannaphila insularis	0	0	4	100.0
Dythemis nigra	0	0	6	100.0
Orthemis cultriformis	0	1	13	96.4
Erythemis haematogastra	0	1	11	95.8
Micrathyria atra	**0**	**36**	**310**	**94.8**
***Perithemis* n. sp.**	**0**	**15**	**25**	**81.3**
Micrathyria pseudeximia	1	1	2	68.8
Micrathyria mengeri	**18**	**118**	**31**	**56.6**
Nephepeltia phryne	**7**	**15**	**1**	**44.6**

Perithemis. There were significant differences in the distribution of these species across the three artificial perch heights, both as a group ($\chi^2 = 308.291$, df = 6, $p < 0.001$) and in pair-wise contrasts: *M. atra* used taller perches more frequently than *Perithemis* ($\chi^2 = 22.956$, df = 1, $p < 0.001$; 2 × 2 table used because neither species used 25 cm perches), *Perithemis* tended to use taller perches than *M. mengeri* ($\chi^2 = 32.861$, df = 2, $p < 0.001$), and *M. mengeri* tended to use taller perches than *N. phryne* ($\chi^2 = 8.447$, df = 2, $p < 0.015$).

Mean male perch height on artificial perches was significantly correlated with mean perch height on natural perches, both across the entire community (including all species with pooled observations on natural perches, r = 0.717, df = 8, $p = 0.015$), and the six species for which means could be calculated on marked individuals (r = 0.817, df = 5, $p = 0.015$).

The mean male perch height of species was strongly correlated with species body size (mean forewing length), using pooled natural perches (r = 0.753, df = 9, $p = 0.006$), means based on marked individuals (0.863, df = 5, $p = 0.013$), or mean perch heights on artificial perches (r = 0.778, df = 8, $p = 0.007$).

Interspecific interactions involving *M. atra* and *M. mengeri*, *N. phryne*, and *Perithemis* were consistent with the hypothesis of a size-dependent competitive hierarchy. The largest of the four, *M. atra*, attacked perched individuals of the three smaller species more frequently – and large conspecifics less frequently – than expected by their relative abundances ($\chi^2 = 13.57$, df = 3, p

< 0.01; Figure 3a). Perched *M. atra* chased conspecific intruders more frequently, *M. mengeri* at the same rate, and smaller species less frequently than expected by their relative frequencies ($\chi^2 = 24.03$, df $= 3$, $p < 0.001$; Figure 3b). The intermediate *M. mengeri* attacked conspecifics and the larger *M. atra* less frequently – and the smaller *Perithemis* more frequently – than expected by their relative abundances ($\chi^2 = 10.77$, df $= 3$, $p < 0.05$; Figure 3c). *Micrathyria mengeri* chased the larger *M. atra* less – and conspecifics and *N. phryne* more – than expected by their relative abundances ($\chi^2 = 22.73$, df $= 3$, $p < 0.001$; Figure 3). Chases by the two small species were too rare to analyze, and they were never observed attacking perched individuals of any species.

These interspecific interactions were largely confirmed in the decoy experiment, but aggression was also highly dependent on the height of the decoy (Figure 4). When decoys were at 100 cm, *M. atra* attacked *M. mengeri* decoys at a significantly higher rate (23 attacks on five decoys) than conspecifics (24 attacks on 10 decoys, $\chi^2 = 16.01$, df $= 1$, $p < 0.001$). However, when decoys were at 50 cm, they were almost ignored by *M. atra* males (one of 48 attacks; $\chi^2 = 46.04$, df $= 1$, $p < 0.001$; N $= 15$ decoys at both heights). Attacks by territorial *M. mengeri* showed a different pattern: all 33 attacks fell on decoys at 50 cm ($\chi^2 = 27.00$, df $= 1$, $p < 0.001$), and *M. atra* and *M. mengeri* decoys were attacked at the same rate ($\chi^2 = 0.128$, df $= 1$, $p > 0.05$).

Discussion

Species exhibited the well-documented correlation between male body size and mean perch height found in other temperate and tropical libellulid communities (Moore, 1991; Resende & De Marco, 2008; Warren, 1964; Worthen, 2017; Worthen & Jones, 2006, 2007). Perch height selection was largely independent of substrate type; species exhibited similar mean perch heights and similar pattern among species on both artificial and natural perches. In addition, these patterns were largely the same in analyses that accounted for individual differences or pooled across individuals. This corroborates a previous study suggesting that, if sample sizes are large, marking individuals is not necessary for resolving differences in perch height among species (Worthen & Hoke, 2018).

There were a few differences in these communities between the dry season (Worthen, 2017) and wet season (this study). First, there was a dramatic change in community membership; only four of 12 dry season species were also present in the wet season. As such, the correlation between male body size and perch height holds across seasonally different communities in the tropics. Two of the four species found in both seasons, *O. cultriformis* and *M. atra*, perched at the same height in the two surveys. The perch heights of the other two species flip-flopped; *C. insularis* perched at 300 cm and *L. herculea* perched at 200 cm in the dry season (Worthen, 2017), but *L. herculea* perched at 300 cm and *C. insularis* perched at 200 cm in the wet season. Without replication of study sites in each season, it is improper to attribute these differences to seasonal changes in behavior; they may be due to differences in the frequency of suitable perches at different heights at the two sites. In the 2016 survey, *L. herculea* perched with equal frequency on downed tree branches at lower heights and branches of living trees at taller heights. In the 2017 survey, there were few downed branches in the wetland, limiting *L. herculea* to taller perches. The behavior of *C. insularis* could be a function of relaxed interspecific aggression. Immature male *C. insularis* look very similar to female *O. cultriformis*, and the unusually high perch height exhibited by *C. insularis* might be a strategy for avoiding the aggressive advances of *O. cultriformis* males (Worthen, 2017). Both species were far less abundant in the 2017 wet-season survey; no aggressive interactions between these species were observed and the only male

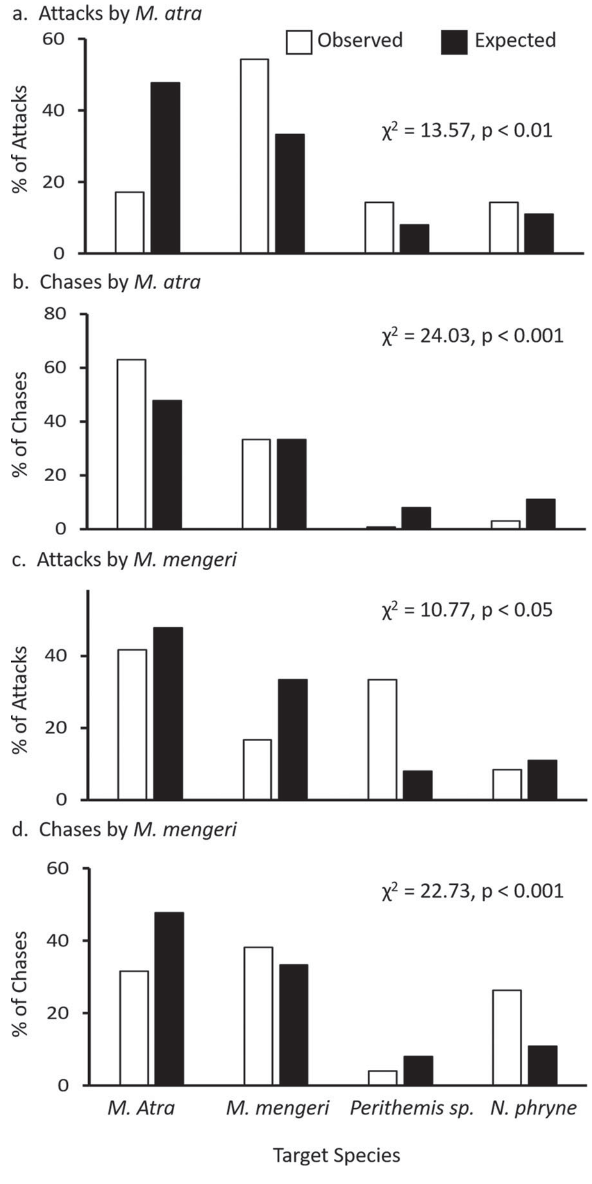

Figure 3. Comparisons of the observed frequencies of aggressive interactions by *Micrathyria atra* and *Micrathyria mengeri* on other ('target') species with expected values based on relative abundances of these species. ('Chase' = sortie by a perched individual against an intruder of a target species; 'Attack' = aggression against a perched individual of a target species.)

C. insularis I observed were mature, slate-blue males that are easily distinguished from brown *O. cultriformis* females. It is possible that reduced aggression allowed *C. insularis* males to perch at a lower height more typical for their body size. Or, there may be developmental or seasonal differences in perch-height selection.

Seasonal changes in community composition and activity patterns may be important predictors of changes that could occur in the wake of climate change. For example, in a study in California, warm-season species and opportunistic species increased in site occupancy from 1900 to 2013 while habitat specialists and cold-adapted species declined (Rapacciuolo, Ball-Damerow,

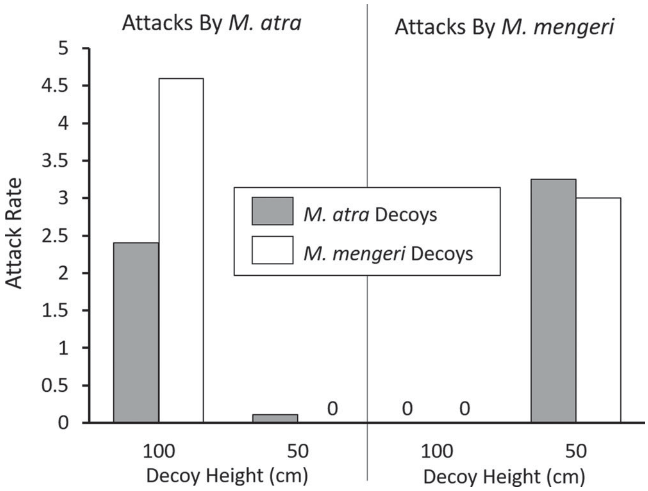

Figure 4. Attack rates (mean attacks/replicate) by territorial *Micrathyria atra* and *Micrathyria mengeri* on decoys of these species placed at different heights. (See text for statistical comparisons.)

Zeilinger, & Resh, 2017). Describing seasonal changes in community composition may provide insight into the species that will be most affected by changes to the duration or intensity of the rainy season in the tropics; particularly the univoltine species that are more dependent on this seasonal rainfall.

Another anomaly was the high perching behavior by the *Perithemis* species, that perched much higher than the other small species (*N. phryne* and *M. pseudeximia*) and higher than the decidedly larger *M. mengeri*. In the temperate zone, congener *Perithemis tenera* Say uses perches at 10–20 cm, consistent with their small body size (Switzer & Walter, 1999; Worthen & Patrick, 2004; Worthen & Jones, 2006, 2007). In the neotropics, *Perithemis mooma* Kirby also perches low (pers. obs.). The *Perithemis* species observed in this study may perch high due to competitive displacement by *P. mooma*, which also occurs at La Selva, but *P. mooma* was rarely observed at this or other wetlands during this sampling period. They might perch high to increase their view of the pools; tall grasses were the dominant vegetation type, there were few perches in the 10–20 cm range, and the grass was very thick – affording a poor view of pools from low vantage points. However, *Nephepeltia phryne* perched low and mated successfully. Visibility may be more important for this bright orange species, for intraspecific territorial display or mate acquisition. In any case, the unusual behavior of this species, especially relative to morphologically similar congeners, is intriguing and invites further study.

The last goal of this study was to determine whether the patterns of perch-height selection by the most abundant species were driven by a size-dependent competitive hierarchy, in which larger species displace smaller species from preferred niches (Khelifa, et al., 2013; Moore, 1964; Pezalla, 1979; Rehfeldt & Hadrys, 1988; Worthen & Jones, 2006, 2007; Worthen & Morrow, 2016). Attacks by *M. atra* on perched individuals in both observational and experimental settings were consistent with this hypothesis. In both circumstances, *M. atra* attacked the smaller *M. mengeri* at higher rates than conspecifics. The lower attack rate on conspecifics may be a function of similar size, but it could also be a function of the tendency of residents to win territorial battles between conspecifics (Parr, 1983; Resende, 2010). It may be easier and safer to displace a smaller species from an attractive territory than to try and displace a resident conspecific. The attack rates in the experiment were also strongly affected by perch height, with *M. atra* largely ignoring all decoys placed at 50 cm. Again, this is consistent with predictions of the size-dependent competitive hierarchy: *M. mengeri* was attacked severely when it perched at the height preferred by the larger *M. atra*, but found refuge from interspecific attacks by perching lower.

Attacks by *M. mengeri* were also consistent with the size-dependent competitive hierarchy hypothesis. In the observational study, this species attacked the larger *M. atra* and resident conspecifics less – and attacked the smaller *Perithemis* species more – than expected by their relative abundances. Again, displacing smaller species may be easier than displacing larger species or resident conspecifics. The experiment showed that this pattern was again affected by perch height, with *M. mengeri* only attacking individuals perched at 50 cm. So, in this experiment, perch height partitioning eliminated all interspecific interactions between these two species.

Chases by *M. atra* and *M. mengeri* were also consistent with a size-dependent competitive hierarchy, if a chase by a perched territorial male indicates a perceived threat and the necessity of territorial defense. The largest species, *M. atra*, preferentially initiated territorial sorties against conspecifics (that obviously pose a territorial threat). Again, as the residents, these perched males have a higher probability of winning an intraspecific contest than the conspecific intruder and should engage and drive out the intruder to retain their territory. Other species were chased at decreasing frequencies relative to their size and abundance, perhaps because these species represented progressively decreasing threats. Chasing males of other species – that are not directly competing for mates and that perch at different heights – is energetically wasteful and should be selected against unless they are competing for food resources or are interfering with mating (Drury, Okamoto, Anderson, & Grether, 2015; Murray, 1981; Tynkkynen, Kotiaho, & Svensson, 2008). This should be particularly true for intruders larger than the territorial male. As predicted, the intermediate *M. mengeri* chased larger *M. atra* less frequently – and conspecifics and *N. phryne* more frequently – than predicted by relative abundances. Again, the perched residents should defend their territory against conspecifics but avoid confrontations with larger species.

In conclusion, although the composition of this wet-season community was different from its dry-season counterpart, the relationship between perch height and male body size was confirmed. In addition, these species-level contrasts are significant whether individual differences are accounted for or not. And, patterns of aggression between species are consistent with the hypothesis that relationship between perch height and body size is maintained by a size-dependent competitive hierarchy.

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